EFFACED STYGINID TRILOBITES FROM THE SILURIAN OF NEW SOUTH WALES

by D. J. HOLLOWAY *and* P. D. LANE

ABSTRACT. Eight species of illaenimorph trilobites belonging to five genera of the Styginidae are described from limestones of the mid–late Wenlock to Ludlow Mirrabooka Formation and its stratigraphical equivalents in the Orange district, New South Wales. The morphology of illaenimorph (= effaced) styginids is discussed; the term 'omphalus' is introduced for the socketed, tubercle-like projection present in some genera on the interior of the cranidium at or in front of the anterior end of the axial furrow. Amongst other characters, the gross convexity of the exoskeleton, the form of the rostral plate, the presence of the omphalus, the form of the thorax, and possibly the form of the hypostome are deemed most useful for generic diagnosis; characters used for discrimination at a lower taxonomic level include the proportions of the exoskeleton, the degree of effacement, the pattern of cranidial muscle scars, the size and position of the eye, and the character and disposition of sculpture. New taxa are *Excetra iotops* gen. et sp. nov., *Lalax olibros* gen. et sp. nov., *L. lens* gen. et sp. nov., *Rhaxeros synaimon* sp. nov. and *R. trogodes* sp. nov. *Bumastus* (*Bumastella*) Kobayashi and Hamada is raised to generic status and its diagnosis emended; specimens from New South Wales are assigned to the type species *B. spicula*, which is considered to be synonymous with five other Japanese species assigned to three different genera by Kobayashi and Hamada. *Bumastus* is tentatively recorded on the basis of a single rostral plate; the genus is otherwise known with certainty only from Laurentia and eastern Avalonia. Meraspid transitory pygidia of *Bumastella* and *Lalax* from New South Wales are up to eight times larger than those of other styginids with well documented ontogenies; transitory pygidia of large size are known also in some other Silurian effaced styginids, and it is suggested that the phenomenon may result from neoteny. The assumption that sexual maturity in trilobites coincided with the meraspid–holaspid transition is refuted. The effaced styginids from New South Wales show strong faunal affinity with those from the Upper Wenlock or Lower Ludlow of Japan.

TRILOBITES are abundant in Silurian limestones west of the city of Orange in central western New South Wales. Few of the species have been described, although they constitute the most diverse and best preserved Silurian trilobite faunas known from Australia. Although at least nine major groups of invertebrates are present in the limestones, the largely disarticulated elements of trilobite exoskeletons are predominant, and most of them are effaced (illaenimorph) forms belonging to the Styginidae. Faunas of this type also occur in lithologically similar relatively pure limestones of Silurian age elsewhere in the world, and were named the 'Styginid-Cheirurid-Harpetid Assemblage' by Thomas and Lane (1998, p. 447, figure 36.1–36.2), who described the lithology in which it occurs, and its stratigraphical and geographical distribution. The reasons for the dominance of effaced trilobite elements in such assemblages are not known; large and small elements of trilobites occur together, and with large and small specimens of other invertebrate groups (ostracodes and brachiopods, respectively with dimensions as little as 2 mm and up to 50 mm), so that hydrodynamic sorting seems not always to be a factor. In some cases it might have been; some 'nested' occurrences of effaced cranidia and/or pygidia were noted, for example of *Rhaxeros trogodes* from locality PL1996. The effect upon the aspect of the association as preserved of discarded exuviae cannot be assessed; however, the commonness of this type of association in rocks ranging from Ordovician to Permian indicates that effaced trilobites might have been the dominant forms in life.

In the present paper, the effaced styginids from only the mid to late Wenlock and Ludlow limestones of the Orange district sequences are described.

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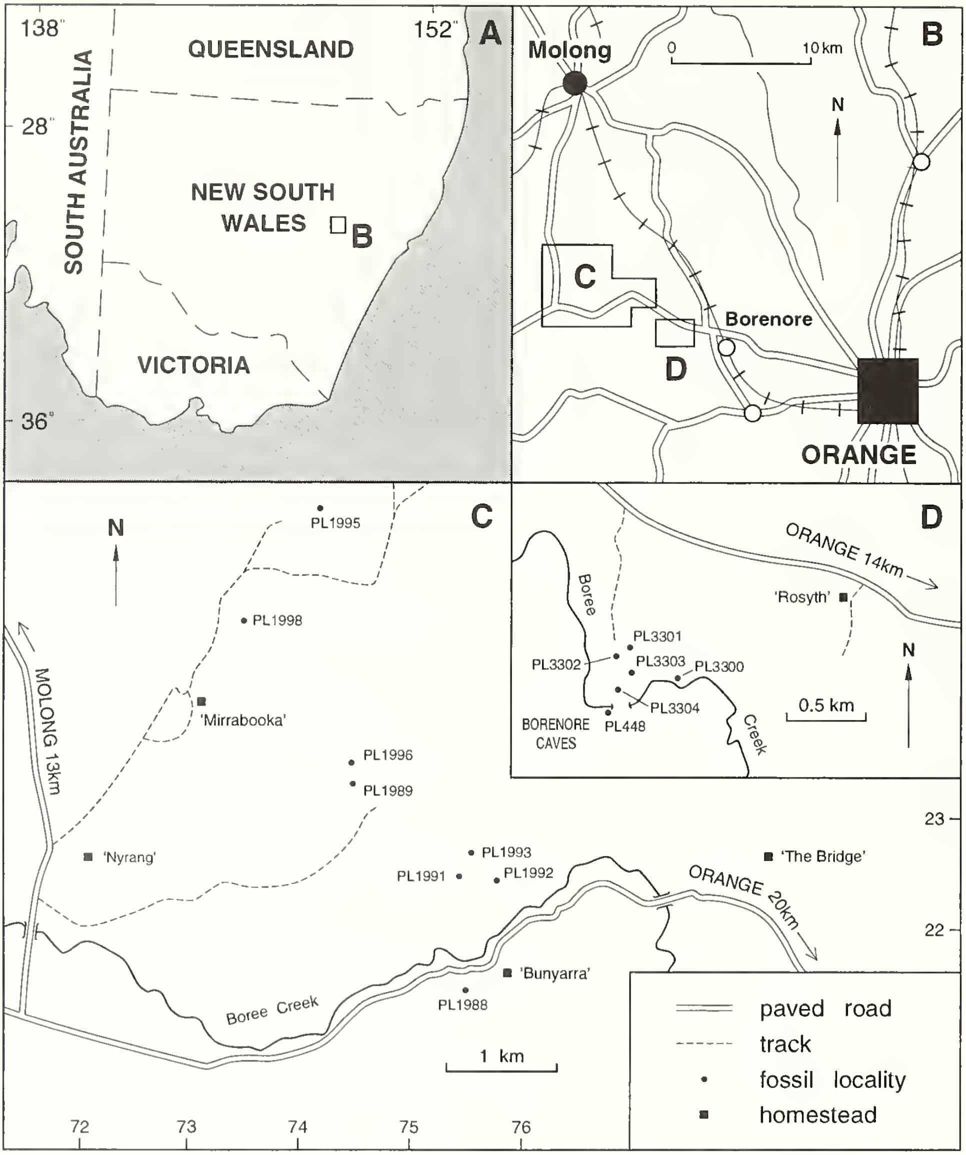


TEXT-FIG. 1. A, South-eastern Australia; approximate area of Text-figure 1B indicated by square. B, general area from which the trilobites were collected. C–D, location of fossiliferous localities.

STRATIGRAPHY

The Silurian sequence in the area between Borenore and Molong, 20–30 km west-north-west of Orange (Text-fig. 1), is characterized by marked and complex changes in lithofacies which, together with the geographically restricted nature of previous geological mapping, has led to the recognition of a variety of stratigraphical units in different parts of the area (Text-fig. 2).

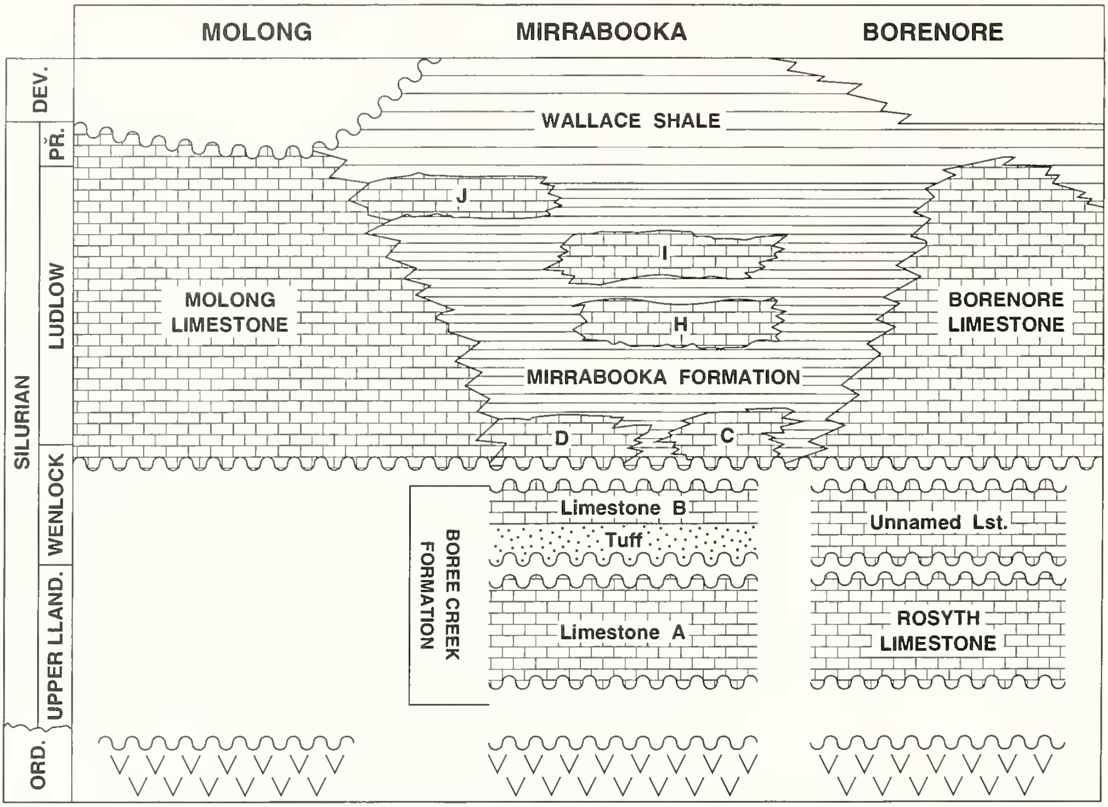
In the western part of the area, near 'Mirrabooka' homestead, the lowermost Silurian unit is the Boree Creek Formation (Sherwin 1971*a*, p. 210), an impure limestone up to 60 m thick (Sherwin and Pickett, *in* Pickett 1982, p. 141) which unconformably overlies late Ordovician andesitic volcanics. The Boree Creek Formation was divided by Sherwin (1971*a*) into lower and upper limestone units, informally named Limestones A and B respectively, separated by a calcareous tuffaceous sandstone referred to as the 'tuffaceous trilobite bed'. A possible disconformity between Limestone A and the 'tuffaceous trilobite bed' was considered by Sherwin and Pickett (*in* Pickett 1982, p. 140) to be probably of only very local significance, and not to represent a significant break. These authors also expressed doubts about the lateral extent of the lithological subdivisions of the Boree Creek Formation; observations by DJH suggest that the subdivisions can be recognized only locally, that the lithology of the 'tuffaceous trilobite bed' is only the result of decalcification of the limestone, and that trilobites are not restricted to the middle part of the formation. Conodonts from the Boree Creek Formation were correlated by Bischoff (1986, p. 36; text-fig. 8) with the latest Llandovery to early Wenlock *amorphognathoides* and *ranuliformis* biozones.

Disconformably overlying the Boree Creek Formation is the Mirrabooka Formation. This consists of 500 m of predominantly fine sandstones and siltstones but also includes several lenticular limestone bodies that were referred to by Sherwin (1971*a*) as Limestones C, H and I. The following graptolite species from near the base of the Mirrabooka Formation were recorded by Pickett (1982, p. 147): *Pristiograptus meneghini*, *Monoclimacis* cf. *flemingi*, *M.* cf. *flumendosae*, *Dendrograptus* sp. and *Dictyonema* sp. – which are considered to represent a mid to late (but not latest) Wenlock age. The age indicated by an assemblage (*Bohemograptus bohemicus*, *Lobograptus* '*scanicus*', *Linograptus posthumus* and *Dictyonema* sp.) from about the horizon of Limestone I (Text-fig. 2), in the upper part of the formation is equivocal; correlation with the Ludlow *scanicus* and *leintwardinensis* biozones was suggested (Pickett 1982, p. 147), but Dr D. Loydell (pers. comm.) suggests that although the Ludlow is indicated, the named species are not all known to occur stratigraphically together elsewhere, and re-examination of the fauna should be undertaken.

Overlying the Mirrabooka Formation with apparent conformity are up to 400 m of shales and siltstones that are commonly olive green or red; they were assigned by Sherwin (1971*a*, p. 219) to the Wallace Shale, the type locality of which lies some 25 km to the south. In the 'Mirrabooka' area the formation also contains pods of limestone up to 250 m long, and a boulder bed and exotic blocks of Ordovician sediments and volcanics. The graptolites *Monograptus* cf. *ultimus* and *M. bouceki*, indicative of the Upper Ludlow, occur in the lower part of the formation (Byrnes, *in* Pickett 1982, p. 154), and the upper part is considered to extend into the Devonian.

In the eastern part of the area, just west of Borenore, the Rosyth Limestone (Walker 1959, p. 42) is equivalent to at least part of the Boree Creek Formation. Problems with the definition of the Rosyth Limestone were discussed by Pickett (1982, p. 161), who restricted the name to the lowermost part of the sequence, which consists of richly fossiliferous limestones and calcareous shales with a thickness of 50 m to more than 100 m. Overlying these strata, apparently disconformably, are 100 m of unnamed lithic arenites, shales and bedded limestones. These are in turn overlain disconformably by the 600 m thick massive white, grey and red limestones of the Borenore Limestone, which is equivalent to the Mirrabooka Formation and probably the lowermost Wallace Shale. Bischoff (1986, p. 38; text-fig. 8) reported conodonts of the early Wenlock *ranuliformis* Biozone in the lower part of the Borenore Limestone; it is possible, however, that the specimens did not come from this formation but from the underlying unnamed limestone unit mentioned above.

To the north of 'Mirrabooka', towards Molong, the Mirrabooka Formation grades into the Molong Limestone (Adrian 1971, p. 193), which directly overlies late Ordovician andesitic volcanics with unconformity, and is unconformably overlain by Late Devonian sandstones. Several discrete limestone bodies occurring to the south of the main outcrop area of the Molong Limestone in the vicinity of 'Mirrabooka' homestead were referred to by Sherwin (1971*a*) as Limestones D–G and J; these were considered by Sherwin (1971*a*, p. 212) to be southern extremities of the Molong Limestone, but Pickett (1982, p. 147) assigned them to the Mirrabooka Formation. The stratigraphical range of the Molong Limestone is uncertain, but the upper part is believed to be equivalent to part of the Wallace Shale and the lower part may contain equivalents of the Rosyth Limestone (Pickett 1982, p. 148).



TEXT-FIG. 2. General stratigraphy of the collection area; modified from Pickett (1982, fig. 18). Abbreviations: Lst. = limestone; Tuff. = tuffaceous trilobite bed of Sherwin (1971*a*); LLAND. = Llandovery; PŘ = Přídolí.

TRILOBITE FAUNAS

The earliest record of trilobites from the area was by de Koninck (1876) who identified *Illaenus wahlenbergi* Barrande?, *Bronteus partschi* Barrande and *Harpes ungula* Sternberg from Borenore Caves, in strata now assigned to the Borenore Limestone. Etheridge (1909) assigned specimens from a similar horizon in the same area to his earlier established species *Illaenus johnstoni*. Etheridge and Mitchell (1917) described the new species *Bronteus angusticaudatus* from the Borenore Limestone south of Borenore Caves, and also *B. mesembrinus* and *B. molongensis* from 'limestone-beds adjacent to Molong', a locality that could refer either to the Molong Limestone or to the Early Devonian Garra Formation. Other trilobites to have been recorded from the Borenore Limestone are *Calymene*, *Encrinurus* and *Sphaerexochus* (Süssmilch 1907; Campbell *et al.* 1974); Dun (1907, p. 265, pl. 40, fig. 7) also identified *Phacops*, but the specimen illustrated is an encrinurid pygidium.

From the Silurian sequence below the Borenore Limestone just to the east of Borenore Caves, Fletcher (1950) described the new species *Dicranogmus bartonensis* (= *Trochurus bartonensis*; see Thomas and Holloway 1988, p. 221), *Encrinurus borenorensis* (= *Batocara borenorense*; see Edgecombe and Ramsköld 1992, p. 259, and Holloway 1994, p. 255) and *Phacops macdonaldi* (= *Ananaspis macdonaldi*; see Holloway 1980, p. 63), as well as *Phacops crossleii* Etheridge and Mitchell. Also present in Fletcher's collections, although not recorded by him, is a species of *Youngia* (Holloway 1994, p. 244). The precise locality from which the material was collected is unknown, but the occurrence of some of the same species in the Boree Creek Formation suggests that the material came from a similar stratigraphical level.

From the Boree Creek Formation, Sherwin (1971*a*, fig. 8) listed the trilobites *Bumastus*, *Decoroproetus*?, *Ananaspis macdonaldi*, *Batocara borenorense*, *Trochurus bartonensis* and *Dicranurus*, and Sherwin (1971*b*) described *Acernaspis*? *oblatus* (a junior synonym of *Ananaspis macdonaldi*; see Holloway 1980, p. 64). Work in progress indicates that the trilobite fauna of this formation includes at least 24 other genera belonging to the families Styginidae, Proetidae, Scharyiidae, Brachymetopidae, Cheiruridae, Staurocephalidae, Calymenidae, Lichidae and Odontopleuridae.

The most abundant trilobite faunas in the overlying Mirrabooka Formation occur in limestones H and I, from which Sherwin (1971*a*, fig. 8) listed *Scutellum*, *Bumastus* sp. B, *Bumastus* sp. C, *Kosovopeltis*, *Decoroscutellum* cf. *molongensis* (Etheridge and Mitchell), *Decoroproetus*? and *Cheirurus*. Apart from the effaced styginids that are the subject of the present work, preliminary investigations on the remaining trilobites indicate that the fauna is at least as diverse as that of the underlying Boree Creek Formation, with representatives of the same families. In addition to the trilobites, other invertebrates present in the Mirrabooka Formation include brachiopods, gastropods, bivalves, rostroconchs, ostracodes, ?stromatoporoids, corals, and pelmatozoan debris.

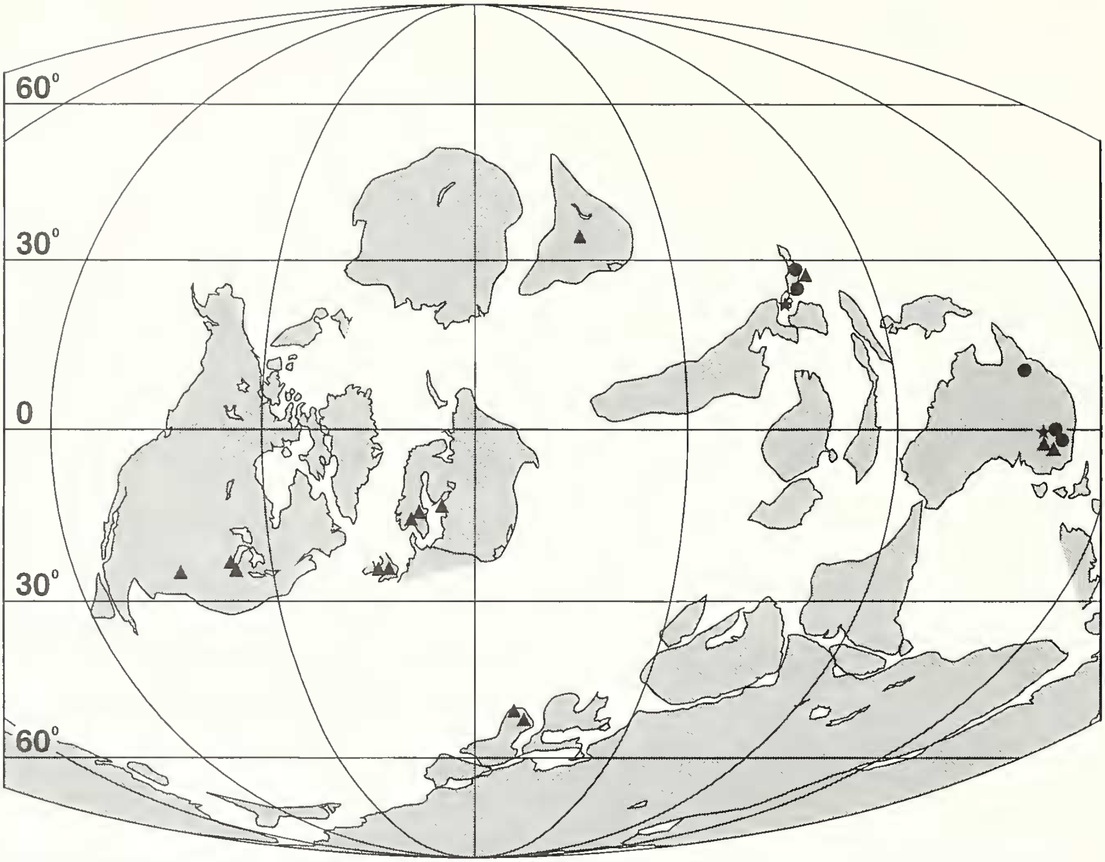
From siltstones just above the base of the Wallace Shale near 'Mirrabooka' homestead, Sherwin (1968) described the trilobite *Denckmannites rutherfordi*, and also recorded *Encrinurus mitchelli* (Foerste) and an indeterminate odontopleurid.

MATERIALS, METHODS AND LOCALITIES

The material is preserved as largely dissociated exoskeletal elements in indurated limestones, which vary from predominantly white to pale grey, pink or, in the case of the Borenore Limestone, red. The cuticle of the trilobites is invariably present and usually adheres preferentially to the internal mould. The matrix is commonly sparry calcite, although sugary-textured and micritic patches occur; mechanical exposure of the exoskeletal elements by Vibrotool is normally relatively easy since the matrix readily parts from the outer surface of the cuticle. Removal of the cuticle from the internal mould, which is necessary to expose features of its internal surface, is correspondingly difficult.

Localities. The trilobites were collected from the following horizons and localities; the localities are marked on Text-figure 1. The PL prefix to locality numbers refers to the Museum of Victoria invertebrate fossil locality register. Grid references apply to the Molong 8631-I & IV and Cudal 8631-II & III 1:50,000 topographic sheets (1st edition) published by the Central Mapping Authority of New South Wales.

1. Limestone H, about middle of Mirrabooka Formation:
   PL1989, GR FD74502330;
   PL1996, GR FD74502350.
2. Limestone I, upper half of Mirrabooka Formation:
   PL1991, GR FD75452250;
   PL1992, GR FD75802245;
   PL1993, GR FD75552265;
   PL1988, GR FD75452155 (correlation with Limestone I tentative).
3. Limestone J, equivalent to the uppermost part of the Mirrabooka Formation:
   PL1998, GR FD73502480.
4. Borenore Limestone, ?lower half:
   PL448, GR FD80351865;
   PL3301, GR FD80501905;
   PL3302, GR FD804190;
   PL3303, GR FD805189;
   PL3304, GR FD804188.
5. Molong Limestone, horizon indeterminate:
   PL1995, GR FD74202580.



TEXT-FIG. 3. Palaeogeographical map for the Ludlow, showing distribution of *Bumastella* (stars), *Rhaxeros* (solid circles) and *Lalax* (triangles); base map modified from Scotese and McKerrow (1990).

Repository. All illustrated material is housed in the invertebrate palaeontological collections of the Museum of Victoria, Melbourne (NMV).

PALAEOBIOGEOGRAPHICAL IMPLICATIONS

The most significant palaeobiogeographical pattern to emerge from our study is the close affinity of the effaced styginids from New South Wales with those from the Late Wenlock or Early Ludlow limestones of Mt Yokokura, Japan (Kobayashi and Hamada 1974, 1984, 1986, 1987). Two of the genera, *Bumastella* and *Rhaxeros*, are known only from eastern Australia and Japan (Text-fig. 3); however, *Leioscutellum* Wu, 1977, from the Llandovery of China, may be a senior synonym of *Rhaxeros*. *Bumastella* is represented in Australia and Japan by the same species, *B. spicula* (Kobayashi and Hamada, 1974), although it has been recorded from Japan under a number of different names (see below). *Rhaxeros synaimon* and *R. trogodes*, described herein from New South Wales, also possibly occur in Japan (see below). *Lalax* occurs in both New South Wales (*L. olibros* sp. nov., *L. lens* sp. nov.) and Japan (e.g. *L. kattoi* (Kobayashi and Hamada, 1984)) but is more widely distributed, being known also from Bohemia (e.g. *L. bouchardi* (Barrande, 1846)), Norway (e.g. *L. inflatus* (Kiaer, 1908)), Estonia ('*Illaenus* (*Bumastus*) *barriensis*' of Holm 1886; see below), Kazakhstan (*L. bandaletovi* (Maksimova, 1975)), the United Kingdom (e.g. *L. xestos* (Lane and Thomas, 1978*a*)), and the eastern United States (e.g. *L. chicagoensis* (Weller, 1907)).

Work in progress on other elements of the trilobite faunas of the Orange district supports the close affinity with Japan, suggesting the existence of a distinctive eastern Gondwanan fauna during the Silurian.

SEGMENTAL VARIATION IN POSTERIOR TAGMATA OF *BUMASTELLA* AND *LALAX*

Many of the dissociated posterior tagmata of *Bumastella spicula*, *Lalax olibros* and *L. lens* from New South Wales include in their anterior part various numbers of fused segments that appear to be unreleased thoracic segments. These specimens thus have the morphology of meraspid transitory pygidia, but there are two aspects of the specimens that are unusual: (1) they are much larger than meraspid transitory pygidia of other trilobites; and (2) unlike meraspid transitory pygidia of other trilobites, some specimens of *Bumastella spicula* from New South Wales show no correlation between the number of fused segments and size.

Tables 1–2 and Text-figures 4–5 show the size of specimens from New South Wales and number of fused segments present. In *Lalax olibros* the number of fused segments decreases progressively from five to zero as the specimen size increases up to a maximum width of *c.* 9 mm; all specimens larger than this lack fused segments. In *L. lens* the smallest known specimen has just one fused segment, and all other specimens, with maximum widths greater that 7 mm, lack fused segments. In relatively small specimens of *Bumastella spicula* the number of fused segments generally decreases with increasing specimen size up to a maximum width of about 15 mm, at which size no fused segments are present; there are, however, several exceptions to this pattern (see Table 2). The smallest specimen of *B. spicula* has five fused segments whereas a slightly larger one has six, the posteriormost segment having a pleural furrow like the segments in front but lacking an interpleural furrow posteriorly. Most specimens of *B. spicula* with maximum widths of 15 mm or more (11 out of 17 specimens) lack fused segments; the remainder have from one to three fused segments (mostly two), there being no correlation between the number of fused segments and specimen size.

In all three species from New South Wales, the pygidium behind the fused segments is identical in form to that of pygidia lacking them. This indicates that the general reduction in the number of fused segments with increasing specimen size in *Lalax olibros* and at least the smaller specimens of *Bumastella spicula* (maximum widths up to 15 mm) is due to the progressive release of segments into the thorax rather than to effacement. Release of segments into the thorax is also demonstrated by some specimens in which the anteriormost segment is only partially fused (e.g. Pl. 6, fig. 7). Hence the fused segments are protothoracic segments, and the specimens are meraspides according to the definition of Whittington (1957, 1959).

TABLE 1. Numbers of fused thoracic segments in posterior tagmata of *Lalax olibros* sp. nov. and *L. lens* sp. nov., arranged in order of increasing maximum width. For both species, all specimens larger than those listed lack fused thoracic segments.

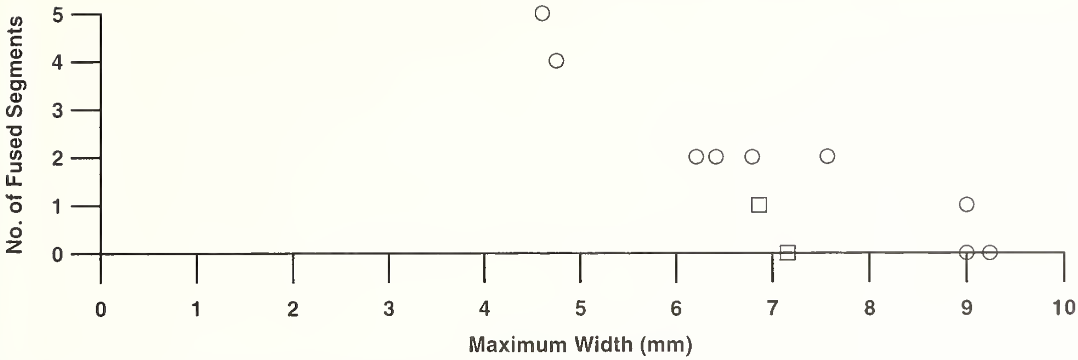
Species	Registration no.	Maximum width (mm)	Fused segments	Figured herein
Lalax olibros	P144944	4·3	5	Pl. 5, fig. 20
	P144810	4·8	4	Pl. 5, fig. 14
	P144808	6·2	2	Pl. 5, fig. 13
	P144809	6·4	2	–
	P144816	6·8	2	–
	P144807	7·6	2	–
	P144806	*c.* 9	1	Pl. 5, fig. 14
	P144844	*c.* 9	0	–
	P144805	9·2	0	–
Lalax lens	P144836	6·9	1	Pl. 6, fig. 7
	P144837	7·1	0	–

TABLE 2. Numbers of fused thoracic segments in posterior tagmata of *Bumastella spicula* from New South Wales, arranged in order of increasing maximum width. All known measurable specimens are listed.

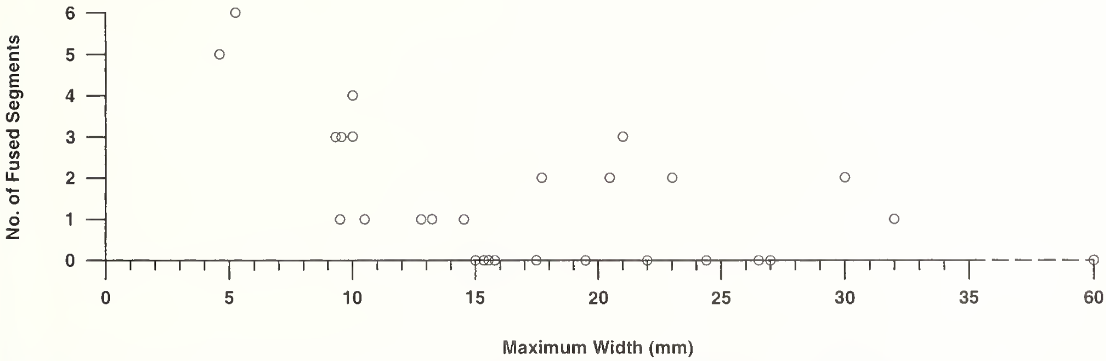
Registration no.	Maximum width (mm)	Fused segments	Formation	Figured herein
P145038	4·7	5	Borenore Lst	Pl. 2, fig. 8
P144943	5·2	6	Mirrabooka Fm	Pl. 2, fig. 12
P144942	9·3	3	Mirrabooka Fm	–
P144940	*c.* 9·5	3	Mirrabooka Fm	–
P145045	*c.* 9·5	1	Borenore Lst	–
P144939	10·0	4	Mirrabooka Fm	Pl. 2, fig. 15
P144941	*c.* 10	3	Mirrabooka Fm	–
P144938	10·5	1	Mirrabooka Fm	Pl. 2, fig. 17
P144969	*c.* 13	1	Molong Lst	–
P145039	*c.* 13	1	Borenore Lst	–
P144968	14·6	1	Molong Lst	–
P145036	15·0	0	Borenore Lst	–
P144937	15·3	0	Mirrabooka Fm	–
P145042	*c.* 15·5	0	Borenore Lst	–
P145037	15·7	0	Borenore Lst	–
P145043	17·5	0	Borenore Lst	–
P145027	17·8	2	Mirrabooka Fm	–
P145035	19·5	0	Borenore Lst	Pl. 2, fig. 5
P144936	20·4	2	Mirrabooka Fm	Pl. 2, figs 3, 6
P144930	21·0	3	Mirrabooka Fm	Pl. 2, figs 9–10
P144965	*c.* 22	0	Molong Lst	–
P144935	*c.* 23	2	Mirrabooka Fm	Pl. 2, fig. 18
P144970	24·3	0	Molong Lst	–
P144934	26·6	0	Mirrabooka Fm	Pl. 2, figs 1–2
P144964	*c.* 27	0	Molong Lst	–
P144933	*c.* 30	2	Mirrabooka Fm	–
P144932	*c.* 32	1	Mirrabooka Fm	Pl. 2, fig. 13
P144931	*c.* 60	0	Mirrabooka Fm	–

Further circumstantial evidence supports the conclusion that pygidia of *Bumastella spicula* with fused segments belong to meraspides. It is provided by two specimens having articulated thoracic segments attached: NMV P144943 (Pl. 2, fig. 12) has four segments in the thorax and six fused segments in the pygidium; and NMV P144930 (Pl. 2, figs 9–10) has seven segments in the thorax and three fused segments in the pygidium. With the possible exception of *Dysplanus*, which was diagnosed as having only nine thoracic segments, all known styginids, effaced or not, for which there is information available have ten thoracic segments in the holaspis. It seems likely, therefore, that NMV P144943 and NMV P144930 exhibit the total number of segments, some thoracic and some still fused, that are going to satisfy the completion of the holaspid thorax (i.e. they are degree 4 and degree 7 meraspides respectively). Of course, because these specimens lack cephala, it is possible that their thoraces are incomplete anteriorly; however, the progressive and marked increase in width (tr.) of the articulating facets on the anteriormost segments present suggests to us that these are from the front of the thorax, and that no segments are missing.

The apparently random occurrence of fused segments in pygidia of *Bumastella spicula* more than 15 mm wide requires further discussion. It might be suggested that, although the fused segments in pygidia less than 15 mm wide are protothoracic segments, those in larger pygidia were added after the release of segments into the thorax had ceased (i.e. after the holaspid stage had been attained). Segments are known to be added to the holaspid pygidium in some trilobites (e.g. *Shumardia*, *Dionide*; see Whittington 1957, p. 442), although the process is unknown in Styginidae. If this process



TEXT-FIG. 4. Plot of number of fused thoracic segments in posterior tagmata of *Lalax olibros* (circles) and *L. lens* (squares) versus maximum width of specimen; all specimens larger than those plotted lack fused segments.



TEXT-FIG. 5. Plot of number of fused thoracic segments in posterior tagmata of *Bumastella spicula* from New South Wales versus maximum width of specimen.

had occurred in *B. spicula*, it would mean that specimen NMV P144930 (discussed above), with seven segments in the thorax and three fused segments in a pygidium 21 mm wide, is not a meraspis displaying the complete number of postcephalic segments, as we have suggested, but a holaspis with the first three thoracic segments broken off. We consider this to be unlikely, in view of the similarity (except for size) between such specimens and smaller transitory pygidia of the species. Other evidence suggesting that the fused segments in the larger pygidia were not added in the holaspid stage is: (1) the fused segments occur at the front of the pygidia, not at the back where new segments are formed; and (2) the number of fused segments in specimens wider than 15 mm does not show a general increase with increasing specimen size.

It is notable that specimens of *Bumastella spicula* more than 15 mm wide with fused segments are known only from the Mirrabooka Formation (locality PL1989; see Table 2) and not from localities in the Borenore and Molong limestones. This suggests that the apparently random occurrence of fused segments in large specimens may reflect either the presence of more than one species within the sample, or the influence of environmental factors that affected the rate of segment release into the thorax in individuals at that locality. However, we can detect no other morphological evidence to support the first possibility, nor is there any evidence (lithological, faunal or taphonomic) that environmental conditions at PL1989 differed from those at other localities where *B. spicula* is found.

In other styginids for which relatively complete ontogenies are known, meraspid transitory pygidia are up to a little more than 3 mm wide (Table 3). Somewhat larger transitory pygidia, up to a little more than 4 mm wide (excluding marginal spines) in a specimen with one protothoracic segment, were recorded in *Kosovopeltis borealis* (Poulsen) by Ludvigsen and Tripp (1990, text-fig.

4F, pl. 4, fig. 5). The largest transitory pygidia of *Lalax olibros* and *L. lens* are almost two to three times the size of the largest transitory pygidium of *Kosovopeltis* (Table 1), whereas the largest transitory pygidium of *Bumastella spicula* is eight times larger (Table 2; however, the smallest pygidium of *B. spicula* without fused segments is three to four times larger than the largest transitory pygidia of *K. borealis*). The smallest transitory pygidia of *L. olibros* and *B. spicula* known, with five fused segments (i.e. meraspid degree 5 if there are ten segments in the holaspid thorax), are between two and four times larger than degree five transitory pygidia of *Scutellum calvum* and *Dentaloscutellum hudsoni* (Chatterton 1971, figs 5A, 7).

TABLE 3. Range in width of transitory pygidia, excluding marginal spines, in some styginids (meraspid degrees 0–9).

Species	Age	Width of transitory pygidia (mm)	Reference
Failleana calva	Ordovician	0·7–2·7	Chatterton (1980, pl. 5, figs 10, 20–21, 30–31)
Kosovopeltis svobodai	Silurian	0·6–3·2	Káchka and Šarič (1991, fig. 6)
Scutellum calvum	Devonian	1·0–1·9	Chatterton (1971, fig. 7)
Dentaloscutellum hudsoni	Devonian	1·0–2·3	Chatterton (1971, fig. 5A)

Meraspid transitory pygidia of large size are also known in other Silurian effaced styginids. A transitory pygidium of *Lalax bouchardi* from Bohemia was figured by Šnajdr (1957, pl. 10, fig. 7); the specimen, which has two protothoracic segments, is *c.* 5·8 mm wide. Transitory pygidia of effaced styginids from Arkansas have also been observed by one of us (DJH); widths of these specimens are 6·3 mm for a specimen of *Lalax* with one protothoracic segment, 4–4·2 mm for specimens of *Illaenoides* with five protothoracic segments, and 5·8 mm for a specimen of *Illaenoides* with three protothoracic segments. This evidence indicates that large meraspides are not unique to the species under discussion here, and in fact the phenomenon may be widespread amongst effaced Silurian styginids. The evolution of such forms with large meraspides from an ancestor or ancestors with normal-sized meraspides may be the result of neoteny (reduced rate of morphological development). Assuming the same rates of growth and moulting in ancestor and descendent, the latter must have undergone a greater number of moults in order to reach a larger size at the same stage of ontogeny. Hence the rate of morphological change (in this case, release of protothoracic segments into the thorax) must have been delayed at each moult in the descendent. If the delay was cumulative at each moult, then throughout ontogeny the descendent form would have fallen further and further behind its ancestor in release of segments into the thorax, accounting for the very large size of some of the meraspides.

Meraspid transitory pygidia comparable in size to those of *Bumastella spicula* are known in the nileid *Illaenopsis harrisoni* from the Arenig of South Wales. Fortey and Owens (1987, p. 197) reported that in this species, which they considered to have the largest merapides of any trilobite, transitory pygidia with one protothoracic segment reach a width of 20 mm, which is two-thirds the size of the largest known transitory pygidia of *B. spicula*. Neoteny was also cited by Fortey and Owens (1987, p. 197) as a possible mechanism for the development of the giant meraspid transitory pygidia of *I. harrisoni*.

A question raised by such giant meraspides is whether they have any bearing on the attainment of sexual maturity (i.e. whether they were biologically adult, although not morphologically complete). From study of the many well-documented and relatively complete trilobite ontogenies known there is no direct evidence for the onset of sexual maturity, and to no organs or structures of the exoskeleton of any trilobite can be ascribed a sexual function. However, sexual maturity is commonly assumed, unjustifiably, to have coincided with attainment of the holaspid stage (e.g.

McNamara 1986, p. 124), although this was defined by Whittington (1957, 1959) in purely morphological terms by the acquisition of the full complement of thoracic segments. It is recognized that protaspid, meraspid and holaspid stages are not developmentally homologous amongst all trilobites (Hughes and Chapman 1995, p. 349), suggesting that sexual maturity may have occurred at different growth stages in different taxa. Whittington (1957, p. 445) noted that some trilobites may increase in length 30- to 40-fold during the holaspid stage (e.g. holaspides of *Isotelus gigas* range from 8–9 mm to 400 mm long, whilst those of *Paradoxides* range from 13·5 mm to over 400 mm). This very large increase in size leads us to suspect that sexual maturity was attained later than the meraspid-holaspid transition in such forms.

Some of the meraspid transitory pygidia of *Bumastella spicula* from New South Wales are amongst the largest specimens of the species known. Assuming that specimens in our collections are representative of the full size attained by individuals of the species, some of these meraspides must have been mature. If so, the release of protothoracic segments into the thorax must have continued in those individuals after maturity, although perhaps at a much slower rate in respect to the moult rate than prior to maturity. If none of the meraspides of *B. spicula* was mature, and assuming that sexual maturity is related to size, it is reasonable to conclude that holaspides smaller than the largest meraspis were also immature. This would mean that the breeding population of the species is virtually unrepresented amongst our collections, a possibility that we believe to be unlikely. We consider, therefore, that sexual maturity and attainment of the holaspid stage are unrelated in *B. spicula*, and that they may be unrelated in many other trilobite species.

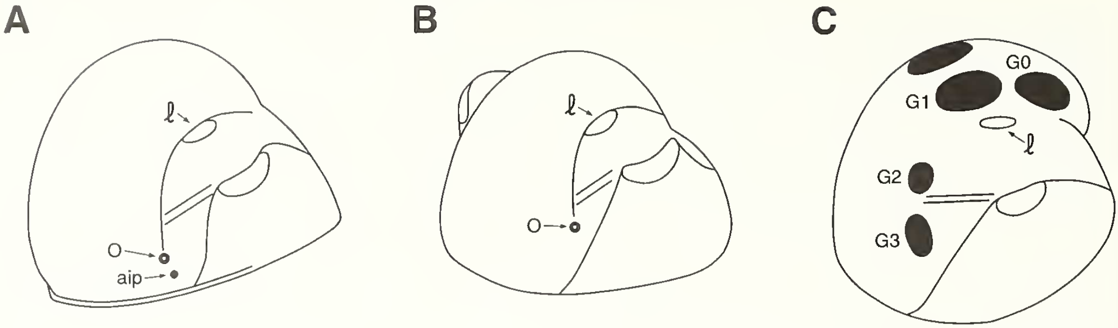
SYSTEMATIC PALAEONTOLOGY

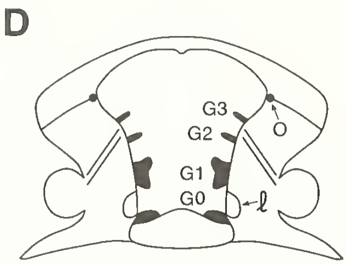
Remarks. Because of the great to extreme effacement of the forms described below, it has not been possible to produce brief generic diagnoses. As diagnosed, genera are distinguished on combinations of characters, all of which are therefore listed. However, it is our belief that the gross convexity of the exoskeleton, the form of the rostral plate, the presence or lack of the 'omphalus' and 'anterolateral internal pit' (see terminology below), and the form of the thorax (width of axis, distance between axial furrow and fulcrum) are of paramount importance in diagnosing genera of effaced styginids. Of possible importance also is the form of the hypostome, which is all too often unknown in the present material and in previously described species of effaced styginids. We consider that the proportions of the exoskeleton, the degree of effacement, the pattern of cranidial muscle scars, and the size and position of the eye (which can, however, vary greatly during ontogeny; see *Bumastella spicula* below) have less taxonomic value, and may be of more use in diagnosing species.

Descriptions commence with the gross morphology of the exoskeleton, followed by descriptions of sculpture, muscle scars and ontogeny where these headings are appropriate. In view of the significant differences in appearance between testiferous and exfoliated specimens of the same species, all descriptions are of the external surface of the exoskeleton, unless otherwise stated.

Terminology. Muscle scars on the glabella are numbered G0, G1, etc. from the posterior forward. The feature associated with the cephalic axial furrow often referred to as the 'lateral muscle impression' is here termed the 'lunette'. The 'holcos' (Helbert and Lane, *in* Helbert *et al.* 1982, p. 132) is the concave zone parallel to and near the lateral and posterior margins of some styginid pygidia. Anteriorly, the holcos is deflected adaxially to unite with an oblique depression running subparallel to the posterior edge of the articulating facet; examination of the ontogenetic development of *Failleana* (Chatterton 1980, pl. 5; Ludvigsen and Chatterton 1980, pl. 1) indicates that this oblique depression is the pleural furrow on the anterior segment of the pygidium.

On the interior of the cranidium of some effaced styginids is a raised boss, commonly with a median depression (often figured as a pit with a central swelling on the internal mould), at which the axial furrow may terminate anteriorly, as in *Cybantyx* (see Lane and Thomas 1978*a*, text-fig. 4f), *Paracybantyx* (see Ludvigsen and Tripp 1990, pl. 1, figs 5–9) and *Lalax* (see Pl. 5, fig. 10); the





TEXT-FIG. 6. Relationship of eye ridge to cephalic muscle impressions and omphalus in various styginids. A, *Cybantyx insignis* (Hall, 1867), based on UC 9902 in the Field Museum of Natural History, Chicago. B, *Lalax chicagoensis* (Weller, 1907), based on holotype, UC 9910; anterolateral pit not distinguishable on specimen. C, *Bumastella spicula* (Kobayashi and Hamada, 1974), based on NMV P144904. D, *Raymondaspis reticulata* Whittington, based on Whittington (1965, pl. 56, figs 1, 3, 6). Abbreviations: aip = anterolateral internal pit; ℓ = lunette; o = omphalus.

term 'omphalus' (latinized from the Greek for navel) is introduced for this structure. The omphalus may be reflected on the exterior of the exoskeleton as a pit or as a small patch devoid of sculpture. Even when the axial furrow cannot be recognized anteriorly, because of a high degree of effacement, the omphalus may be clearly defined and is useful in indicating the transverse extent of the glabella, as in *Lalax* gen. nov. Other effaced styginids in which the omphalus occurs are *Dysplanus* Burmeister, 1843, *Failleana* Chatterton and Ludvigsen, 1976, *Litotix* Lane and Thomas, 1978*a*, *Opsypharus* Howells, 1982 and *Platillaenus* Jaanusson, 1954. Situated just in front of the omphalus, and usually slightly adaxial or abaxial to it, there may be a small pit on the interior of the cranidium (appearing as a node on internal moulds), as in *Lalax* (see Pl. 5, figs 3, 7, 9–10; Lane and Thomas 1978*a*, pl. 3, fig. 14a) and also *Cybantyx*; this pit is here termed the anterolateral internal pit.

The omphalus was described by Ludvigsen and Chatterton (1980, p. 476) as a 'socketed pit' (illustrated as a pitted tubercle in their pl. 1, fig. h) and considered by them to be one of the diagnostic features of Bumastinae (Raymond, 1916; as conceived by Jaanusson 1959). Of the genera normally assigned to the subfamily, however, the omphalus is absent in the type species of *Bumastus*, *B. barriensis* Murchison, 1839, and in *Goldillaenus* Schindewolf, 1924, *Illaenoides* Weller, 1907 and *Thomastus* Öpik, 1953. More recently described effaced styginid genera in which the omphalus is absent are *Bumastella* Kobayashi and Hamada, 1974, *Excetra* gen. nov., *Ligiscus* Lane and Owens, 1982, *Meitanillaenus* Chang, 1974, *Ptilillaenus* Lu, 1962 and *Rhaxeros* Lane and Thomas, 1980.

From its position, the omphalus is not the homologue of the 'fossula', which is defined as lying at the anterior edge of the eye ridge. In *Cybantyx insignis* and *Lalax chicagoensis*, the omphalus is situated well in front of the anterior end of the eye ridge (Text-fig. 6A–B). In *Bumastella spicula* (described below) the eye ridge is directed towards a point between G2 and G3 (Text-fig. 6C); *Bumastella* lacks an omphalus, but in other effaced styginids in which the omphalus is present it is situated level with or in front of G3. Hence, although no fossula is present in these forms or the others under discussion here, the omphalus lies morphologically anterior to where such a structure would be expressed. Chatterton and Ludvigsen (1976, p. 39) stated, however, that in *Failleana calva* the omphalus is situated where '…a very shallow furrow that is posteriorly continuous with palpebral furrow joins axial furrow' (i.e. at the posterior edge of the eye ridge); this statement is not supported by their illustrations (Chatterton and Ludvigsen 1976, pl. 6, figs 6, 39) which show the omphalus lying well in front of the weak furrow defining the anterior edge of the eye ridge.

The omphalus seems to be homologous with the pit (as expressed on the exterior of the exoskeleton) that lies in the axial furrow at or just behind the junction with the lateral border furrow in some non-effaced Ordovician styginids, including species of *Stygina* Salter, 1853, *Raymondaspis* Přibyl, *in* Prantl and Přibyl, 1949 (see Text-fig. 6D) and *Turgicephalus* Fortey, 1980, and also in *Theamataspis* Öpik, 1937 (see Skjeseth 1955, pl. 3, fig. 1; Whittington 1965, pl. 56, figs 3, 7, pl. 59, figs 1, 5–8; Fortey 1980, pl. 6, figs 1–2, 5, pl. 7, figs 1–3, pl. 9, figs 1–3, 5). In *Platillaenus*, the omphalus ('Vordergrube' of Jaanusson 1954, pl. 3, fig. 6) also lies at the junction of the axial and lateral border furrows.

Functionally, the omphalus was apparently involved with the attachment of the hypostome to the cranidium. Jaanusson (1954, p. 548, text-fig. 1, pl. 3, figs 2, 4) showed that in *Dysplanus centrotus* the anterior wing process of the hypostome projects well forward above the cephalic doublure and is in close proximity with the omphalus. Chatterton and Ludvigsen (1976, p. 39, pl. 6, figs 2, 11, 16) described a protuberance similar in form to the omphalus on the inner (dorsal) margin of the librigenal doublure of *Failleana calva*; this librigenal protuberance faces the omphalus and the two are adjacent in a complete cephalon. Although they were unsure of its function, Chatterton and Ludvigsen (1976, p. 39) suggested that the librigenal structure may have been associated with ligament or muscle attachment to the anterior wing of the hypostome, or with the omphalus.

Orientation. In convex to highly convex trilobites, it is difficult to indicate the exact orientation of specimens for description and photography. As applied herein to cephala and cranidia, 'dorsal view' indicates that the posterior margin adaxial to the fulcrum is vertical, 'palpebral view' that the upper edge of the visual surface (or palpebral suture) is horizontal, and 'plan view' that the maximum sagittal length is being shown. For pygidia, 'dorsal view' indicates that the anterior margin adaxial to the articulating facet is vertical, and 'plan view' that the lateral and posterior margins are horizontal (in plan view a little less than the maximum sagittal length of the pygidium is shown). As convexity varies during ontogeny of individual species, and between species, 'plan' and 'palpebral' views are not necessarily identical at all stages of ontogeny and in different species, and in other cases the two views may coincide.

Suborder ILLAENINA Jaanusson, 1959
Family STYGINIDAE Vogdes, 1890

Remarks. The family name is used here in the emended sense of Lane and Thomas (1983, p. 156), who recognized no subfamilial divisions because of the inability at present to recognize phyletic lines of development. Ludvigsen and Tripp (1990, p. 8) retained the division of Styginidae into Stygininae, Scutelluinae and Bumastinae 'as an aid to grouping the large number of genera in the family' but did not indicate which characters could be used as a basis for this subdivision. We consider, however, that the only justification for the recognition of supraspecific taxa is evolutionary relationship. Although also rejecting Ludvigsen and Tripp's concept of styginid subfamilies as taxa of convenience, Adrain *et al*. (1995, p. 726) recognized Scutelluinae and Bumastinae as phylogenetic entities that 'may very likely prove to be monophyletic', but no evidence to support this statement was offered. Nielsen (1995, pp. 295, 320) recently used Stygininae and Bumastinae as subdivisions of Styginidae without any discussion on the characters he regarded as diagnostic.

Genus BUMASTELLA Kobayashi and Hamada, 1974

Type species. By original designation; *Bumastus* (*Bumastella*) *spiculus* Kobayashi and Hamada, 1974 from the Upper Wenlock (or Lower Ludlow), Gomi, Yokokura-yama, Kôchi Prefecture, Shikoku, Japan.

Emended diagnosis. Cephalon extremely convex (sag., exsag., tr.), almost hemispherical; in dorsal profile, posterior margin transverse medially, deflected posteroventrally abaxial to fulcrum towards broadly rounded genal angle. Axial furrow shallow and poorly defined close to posterior margin, not impressed farther forwards. Eye small, in palpebral view placed with posterior edge in transverse line with posterior edge of lunette, in lateral view placed at half height of cephalon; visual surface borne on steep, concave band of librigena. Anterior branch of facial suture gently convergent forwards, posterior branch gently divergent backwards. Rostral plate sub-triangular, lacking posterior flange, convexity in sagittal line greatest anteriorly. Thorax with gently convex axis narrowing markedly backwards; articulating furrows not impressed; pleurae with horizontal portion adaxial to fulcrum widening (tr.) in more posterior segments, as wide (tr.) as or wider than gently downturned portion abaxial to fulcrum. Pygidium wider than long (sag.), much less convex than cephalon, with strongly developed holcos.

Remarks. The above diagnosis is an attempt to characterize the genus allowing for the considerable morphological changes which are seen during ontogeny. These changes, which are outlined below in the section on ontogeny, are partly the reason that we consider the type species to be synonymous with two other species of *Bumastella* and one of *Bumastus* erected by Kobayashi and Hamada (1974) at the same time, and with at least one (and possibly another) form described as possible species of *Illaenoides* by the same authors in a later work (see synonymy of *Bumastella spicula* herein).

Kobayashi and Hamada (1974, p. 50) erected *Bumastella* as a subgenus of *Bumastus*, and diagnosed it as having a 'narrower axial lobe which is clearly separated in thorax from pleurae by pronounced axial furrows. Eyes are very large in comparison with those of *Stenopareia* Holm, 1886 (see Owen and Bruton 1980, pl. 2, fig. 11). Short genal spines are present in the type species.' We consider that, apart from the effacement, *Bumastella* has little similarity with *Bumastus* and is not closely related to it. In our opinion, *Bumastella* has more similarities to *Illaenoides* and *Thomastus* (for comparison with the latter see Sandford and Holloway 1998).

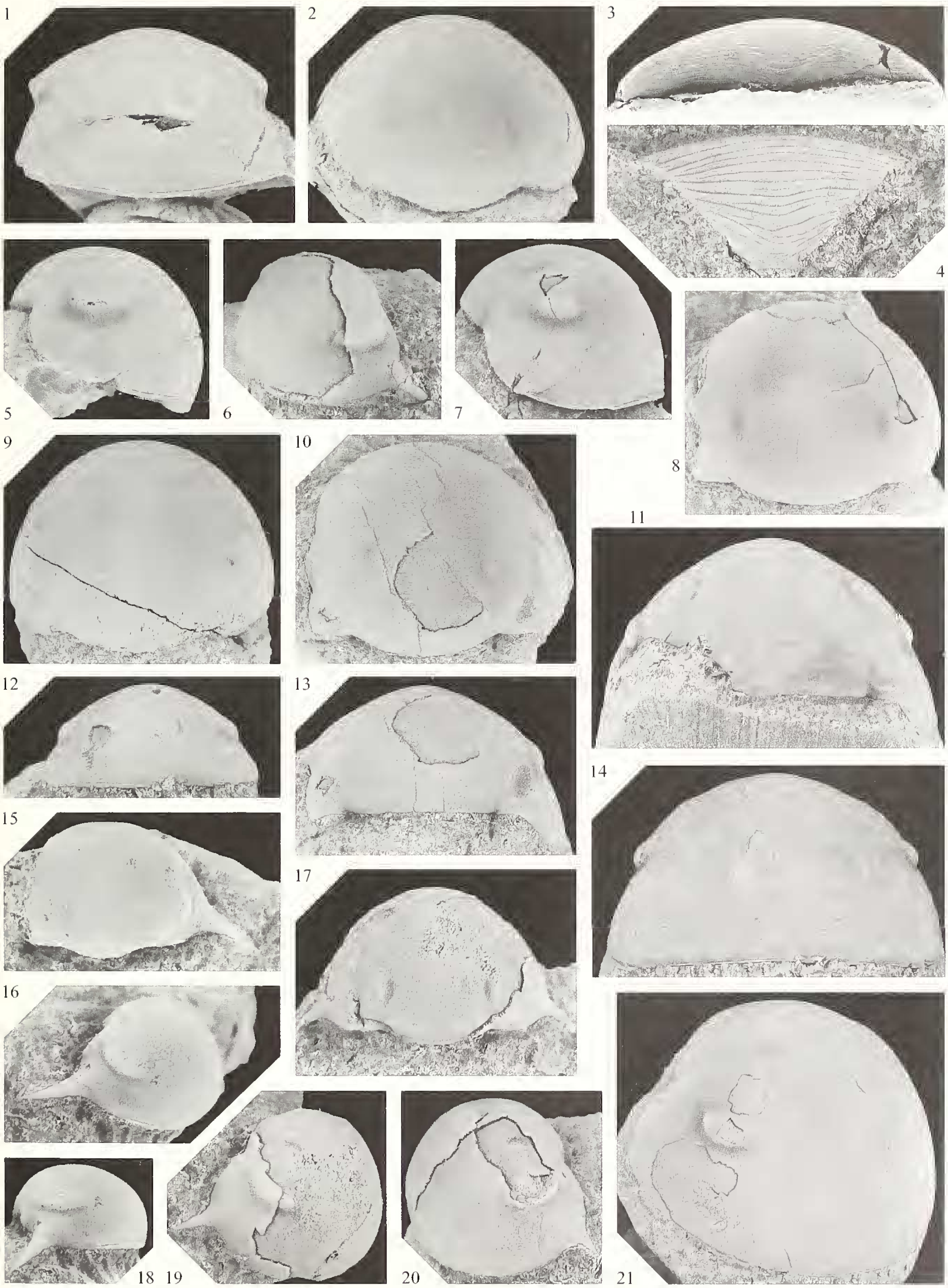
The similarities with *Illaenoides* (type species *I. triloba* Weller, 1907, p. 226, pl. 17, figs 6–9, pl. 19, figs 12–14) from the Niagaran (upper Llandovery or Wenlock) of Illinois include the extreme convexity of the cephalon, the glabella that narrows weakly forwards from the posterior cephalic margin to the lunette, the small eyes, the subparallel anterior branch and weakly divergent posterior branch of the facial suture, and the strong holcos. *Illaenoides* differs from *Bumastella* in that the eyes are even smaller and are situated farther forwards, with the posterior margin in front of the lunette in palpebral view; the posterior cephalic margin is deflected less strongly backwards abaxial to the fulcrum; the rostral plate is lenticular in outline rather than triangular, with connective sutures that are distinctly sigmoidal rather than almost straight; the pleurae on the posteriormost thoracic segments are wider abaxial to the fulcra than adaxially; and the pygidium is longer.

In view of the differences, even from closely related forms, we consider it necessary to raise Kobayashi and Hamada's taxon to generic status.

Stratigraphical range and distribution. Late Wenlock to ?early Ludlow; Japan and New South Wales.

EXPLANATION OF PLATE 1

Figs 1–21. *Bumastella spicula* (Kobayashi and Hamada, 1974); locality PL1989, Mirrabooka Formation, unless otherwise indicated. 1–3, 5, NMV P144906; cephalon, anterior and palpebral views; ×2; ventral view; ×2·5; lateral view; ×2. 4, NMV P144928; rostral plate, ventral view; ×4. 6, NMV P144953; locality PL1995, Molong Limestone; small cephalon, oblique view; ×5. 7–8, NMV P145028; locality PL448, Borenore Limestone; cephalon, lateral and palpebral views; ×1·75. 9, NMV P144907; cephalon, palpebral view; ×3. 10, 13, NMV P144905; cephalon, palpebral and dorsal views; ×1·75. 11, 14, 21, NMV P144904; largest cephalon, dorsal, anterior and oblique views; ×1·75. 12, NMV P144908; small cephalon, anterior view; ×5. 15–16, 18, NMV P144910; smallest cephalon, palpebral, oblique and lateral views; ×6. 17, 19, NMV P144951; locality PL1995, Molong Limestone; small cephalon, palpebral and oblique views; ×4·5. 20, NMV P144950; locality PL1995, Molong Limestone; small cephalon, oblique view; ×4·5.



HOLLOWAY and LANE, *Bumastella*

Bumastella spicula (Kobayashi and Hamada, 1974)

Plate 1, figures 1–21; Plate 2, figures 1–15, 17–18;
Text-figure 6C

1909 *Illaenus Johnstoni* Etheridge; Etheridge, p. 1, figs 1–2 [*non* Etheridge 1896, p. 33, pl. fig. 3].
1974 *Bumastus glomerosus* Kobayashi and Hamada [*partim*], p. 47, pl. 1, figs 3–6, 8 [*non* fig. 7 = *Rhaxeros subquadratus*]; text-fig. 2A.
1974 *Bumastus* (*Bumastella*) *spiculus* Kobayashi and Hamada, p. 51, pl. 2, fig 3; text-fig. 2D.
1974 *Bumastus* (*Bumastella*) *bipunctatus* Kobayashi and Hamada, p. 51, pl. 2, figs 4–9; ?pl. 3, fig. 1; text-fig. 2E.
1974 *Bumastus* (*Bumastella*) *aspera* Kobayashi and Hamada [*partim*], p. 52, pl. 3, figs 3–5 [*non* fig. 6 = *Rhaxeros* cf. *synaimon*]; text-fig. 2F, cephalon only [pygidium = *Rhaxeros* cf. *synaimon*].
1985*a* *Bumastus glomerosus*; Kobayashi and Hamada [*partim*], p. 345.
1985*a* *Bumastus* (*Bumastella*) *spiculus*; Kobayashi and Hamada, p. 345.
1985*a* *Bumastus* (*Bumastella*) *bipunctatus*; Kobayashi and Hamada, p. 345.
1985*a* *Bumastus* (*Bumastella*) *aspera*; Kobayashi and Hamada [*partim*], p. 345.
1985*a* *Illaenoides* (?) *magnisulcatus* Kobayashi and Hamada [*nom. nud.*], p. 345.
?1985*a* *Illaenoides* (?) *abnormis* Kobayashi and Hamada [*nom. nud.*], p. 345.
1986 *Illaenoides* (?) *magnisulcatus* Kobayashi and Hamada, p. 452, pl. 90, fig. 5.
?1986 *Illaenoides* (?) *abnormis* Kobayashi and Hamada, p. 453, pl. 90, fig. 6.
*non*1987 *Bumastus glomerosus*; Kobayashi and Hamada, p. 110, figs 1A, 2.1a–d [= *Lalax*? sp.].

Holotype. University of Tokyo Museum No. 7345; from the Upper Wenlock (or Lower Ludlow); Gomi, Yokokura-yama, Kôchi Prefecture, Shikoku, Japan.

Other material. Approximately 17 cephala, 19 cranidia, 18 librigenae, one rostral plate, six thoracopyga and 26 pygidia (including meraspid transitory pygidia), from PL448, PL1988, PL1989, PL1995, and PL3301–PL3304.

Description. Cephalon almost semicircular in lateral and dorsal views, more than semicircular in anterior and palpebral views; in palpebral view, sagittal length 85 per cent. of maximum transverse width which is level with posterior edge of eye. Axial furrow forming shallow notch in posterior cephalic margin, rapidly dying out just in front of posterior margin but in some specimens very faintly discernible as far forward as lunette, towards which it converges weakly; width of glabella at posterior margin slightly more than half maximum cephalic width. From posterior end of axial furrow, a short (tr.), indistinct furrow is directed laterally and slightly forwards, just in front of narrow (tr.), horizontal portion of posterior fixigenal margin adaxial to fulcrum. Lunette weakly expressed, rather more than 50 per cent. of length of visual surface, situated with anterior edge level with cephalic midlength (sag.) in palpebral view. Fixigena adaxial to palpebral lobe slightly inflated above general transverse convexity (in anterior view); palpebral lobe narrow (tr.), sloping less steeply abaxially than adjacent part of fixigena, length *c*. 20 per cent. of sagittal length of cephalon in palpebral view, placed at 100–150 per cent. its own length from posterior margin; palpebral furrow shallow and poorly defined, weakly curved in palpebral view. Eye ridge (faintly visible in one specimen under the microscope but not in photographs; see Text-fig. 6C) very narrow, running anteromedially from close to front of palpebral lobe towards midway between G2 and G3, but dying out before reaching line of these impressions. Anterior section of facial suture subparallel to sagittal line posteriorly, curving adaxially anteriorly to cut cephalic margin in line (exsag.) with abaxial edge of lunette; palpebral section of suture very gently curved; posterior section diverging gently backwards, almost straight for most of its course but deflected slightly more strongly abaxially near posterior margin. Librigena gently convex exsagittally and weakly convex transversely; visual surface gently convex dorso-ventrally, subparallel sided with rounded anterior and posterior margins; lenses very small and very numerous.

Cephalic doublure steeply inclined, more convex medially than laterally. Rostral plate with maximum width a little more than twice sagittal length, and 50 per cent. of width of cranidium at palpebral lobes. Anterior margin broadly rounded; lateral margins converging backwards at *c*. 110–120°, slightly more strongly near anterior margin than farther back; posterior margin transverse or weakly convex forwards.

Hypostome unknown.

Number of thoracic segments unknown. In a specimen with seven thoracic segments articulated with a meraspid transitory pygidium having three protothoracic segments (Pl. 2, figs 9–10), thoracic axis is 80 per cent.

as wide (tr.) posteriorly as anteriorly, and horizontal portion of pleurae adaxial to fulcrum is twice as wide posteriorly as anteriorly; overall, thorax becomes slightly wider backwards. Axial furrow broad and shallow. Anterior segments with pleurae flexed strongly backwards at fulcrum, and with large articulating facets occupying most of segmental length; more posterior segments successively less strongly flexed backwards at fulcrum but curving forwards slightly distally, with successively smaller articulating facets.

Pygidium more convex sagittally than transversely, semi-elliptical in outline, in plan view sagittal length 70 per cent. of maximum width, which is at posterior outer angle of articulating facet. Anterior margin gently arched forwards across axis, between anterior ends of holcos; anterior width of axis 50 per cent. of maximum pygidial width; short (sag., exsag.) articulating half ring defined by absence of sculpture and by faint articulating furrow abaxially. Articulating facet short (exsag.), occupying *c.* 60 per cent. of width (tr.) of anterior pleural margin; anterior edge of facet with small process situated closer to abaxial than adaxial extremity. Anteriormost pleural furrow strongly developed, joining in a broad curve with holcos which dies out quite suddenly at *c.* 66 per cent. of maximum pygidial length. Doublure occupying *c.* 20 per cent. of sagittal length of pygidium, slightly less convex medially than anteriorly but more steeply inclined.

Sculpture. Cephalon everywhere covered by dense, small and indistinct pits; especially at posterior margin, and for a little way forward on glabella, this pattern of pits has very narrow, irregular, anastomosing furrows superimposed. Near to anterior margin of cranidium, a few weakly developed terrace ridges are present. Lateral and anterior margins of cephalon bear a very narrow but distinct marginal thread. Rostral plate with ten non-anastomosing terrace ridges present on ventral surface; most anterior of these ridges run parallel to anterior margin, medial ones become transverse, and posterior few ridges curve convex backwards to become subparallel to posterior margin.

Thorax and pygidium bear packed indistinct pits like those of cephalon. In addition, distinct terrace ridges are present on and behind articulating facets of thoracic pleurae and pygidium, forming a chevron pattern on lateral parts of pygidium abaxial to the holcos (Pl. 2, fig. 13).

Muscle scars. Glabella bears four pairs, distinguished by weak wrinkling of exterior of exoskeleton in some specimens. G0 and G1 elongated, of similar size and in line exsagittally; G0 situated less than its own length from posterior cephalic margin, extending forwards almost level with posterior edge of lunette in palpebral view; G1 with posterior margin just in front of transverse line through back of lunette and anterior margin opposite front of eye in palpebral view. G2 smallest, sub-circular, slightly more abaxially placed than G1, equidistant from G1 and G3. G3 also sub-circular, slightly larger than G2 (but much smaller than G0 and G1) and placed slightly farther abaxially, about twice as far from anterior cephalic margin as from G2.

Pygidia have two or more pairs of relatively small, sub-circular and poorly defined muscle scars situated anteriorly close to the sagittal line; another pair of larger, sub-circular scars, situated farther from the sagittal line just in front of the pygidial midlength (sag.), is defined by a reticulate appearance of the exterior of the exoskeleton. Surrounding the region of the paired muscle scars laterally and posteriorly, and extending backwards as far as 75 per cent. of the sagittal pygidial length, is a broad, arcuate band of scattered, small (*c.* 0·1–0·2 mm diameter), circular pits, possibly representing muscle attachment sites on the interior of the exoskeleton (Pl. 2, fig. 13)

The smallest meraspid transitory pygidium (Pl. 2, fig. 8), with five protothoracic segments, has a pair of elliptical scars impressed on the interior of the exoskeleton, either side of a small, raised (on internal mould) sub-triangular area apparently representing the axis. These scars are probably the posterior pair described above.

Ontogeny. The above description is based on some of the largest exoskeletal elements from New South Wales, which differ from the smallest growth stages in a number of respects. Morphological changes that occur during ontogeny (apart from the change in number of protothoracic segments in meraspid transitory pygidia; see above) are as follows.

1. The genal spine gradually deceases in length and finally disappears. In the smallest cephalon, with a width of 5 mm (Pl. 1, figs 15–16, 18; librigena 2·5 mm maximum length) the genal spine is 1·6 mm long; on a cephalon 8·2 mm wide (Pl. 1, figs 17, 19; librigena 4·5 mm long) it is 1·4 mm long; on a librigena about 9·5 mm long (Pl. 2, fig. 14) it is developed only as a very short, thorn-like point (the tip of which is broken off); and on a librigena 10·2 mm long (Pl. 2, fig. 11) it is represented by a very small swelling.
2. The cranidium changes from slightly wider than long to slightly longer than wide in plan view.
3. The length of the visual surface changes from about one-third to about one-tenth of the length of the cephalon in plan view.

4. The eye changes in position from less than one-half its own length, to more than its own length from the posterior edge of the cephalon.
5. Overall convexity of the cephalon increases (compare Pl. 1, figs 7, 18), and the cephalic outline in plan view changes from semicircular to circular.
6. Sagittal length of the pygidium increases slightly relative to width.
7. Overall convexity of the pygidium increases.
8. The holcos and anteriormost pleural furrow are very weak in the smallest meraspid transitory pygidia (Pl. 2, figs 8, 12) and become more distinct in larger specimens.

In some other effaced styginids, for example *Bumastus barriensis* (see Lane and Thomas 1978*a*, pl. 4, fig. 6) and *Failleana calva* (see Ludvigsen and Chatterton 1980, pl. 1, figs s–v), a genal spine is present in small specimens but is absent later in ontogeny.

Remarks. Study of the ontogenetic changes in *Bumastella* collected from a single locality (PL1989), discussed above, led us to the conclusion that those Kobayashi and Hamada species we have synonymized, each of which is based on only one or a few specimens (mostly cranidia), all from the Yokokura limestone of Mt Yokokura (possibly the same locality; see Kobayashi and Hamada 1985*a*, p. 345), represent different stages in the ontogeny of a single species. The smallest form available in our collections has the morphology of *B. spicula* (the type species), which is followed by specimens in order of increasing size having the form of *B. bipunctata*, *B. aspera*, '*Illaenoides*?' *magnisulcatus*, possibly '*I.*?' *abnormis*, and finally the largest morph '*Bumastus*' *glomerosus* which Kobayashi and Hamada (1974, p. 47) noted 'is the largest illaenid species in the Yokokura fauna'. The Japanese material, of which we have examined plaster casts, is not as well preserved as that from New South Wales, so that it has not been possible to compare all details, such as sculpture. However, based on a comparison of general proportions and convexity of cranidia during growth, we believe that the latter material is conspecific.

We consider that the pygidium Kobayashi and Hamada (1974) assigned to *Bumastella aspera*, and one of the pygidia they assigned to '*Bumastus*' *glomerosus*, do not belong to *Bumastella* but to two different species of *Rhaxeros* (see discussions of *R. synaimon* and *R. trogodes*).

Three cephala from the Borenore Limestone at Borenore Caves were referred by Etheridge (1909) to his species *Illaenus johnstoni*, originally based (Etheridge 1896) on material from the Ordovician

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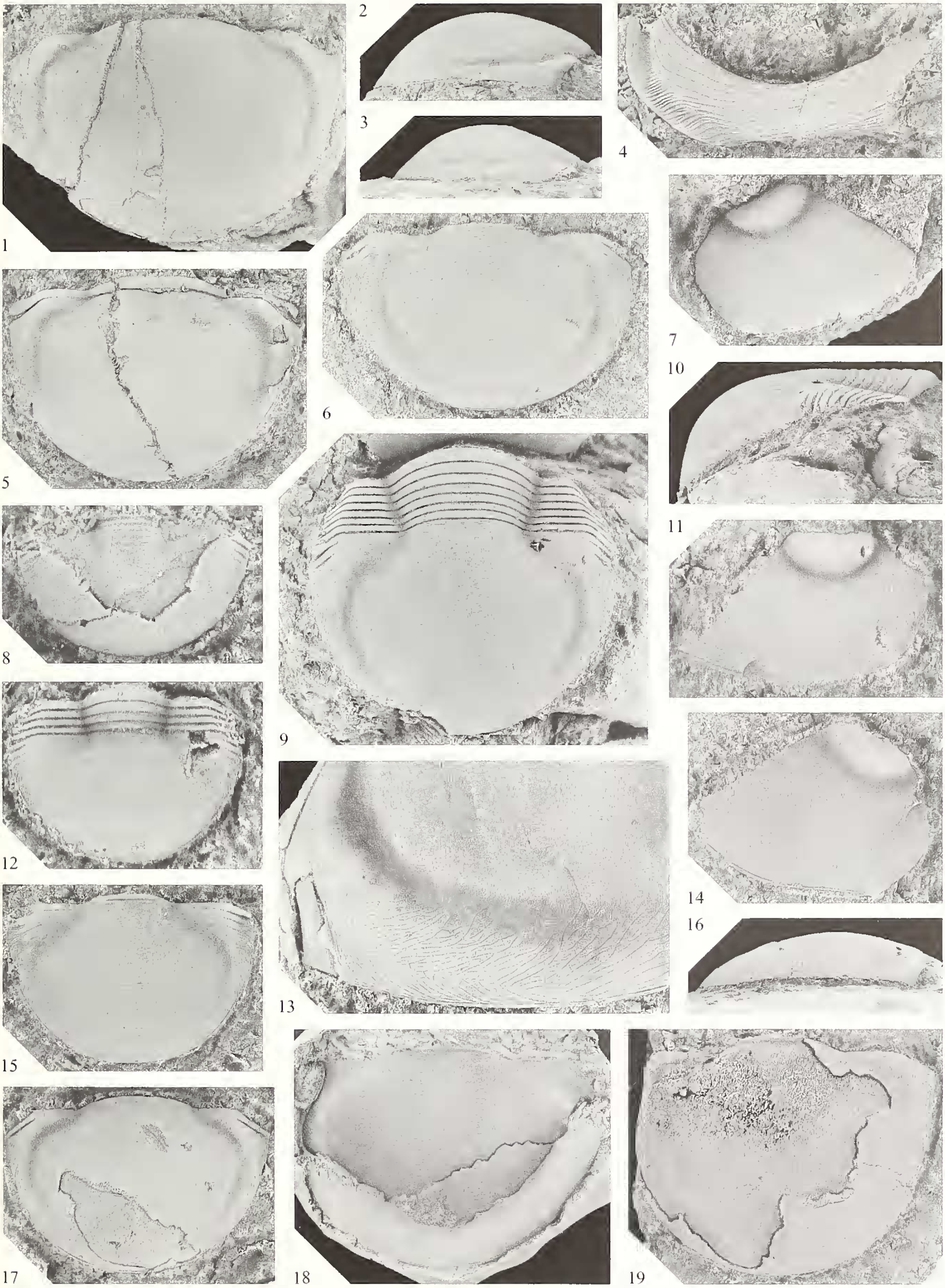
EXPLANATION OF PLATE 2

Figs 1–15, 17–18. *Bumastella spicula* (Kobayashi and Hamada, 1974); locality PL1989, Mirrabooka Formation, unless otherwise indicated. 1–2, NMV P144934; pygidium, dorsal and lateral views; ×2. 3, 6, NMV P144936; transitory pygidium with two protothoracic segments, lateral and dorsal views; ×2·25. 4, NMV P145041; locality PL3301, Borenore Limestone; librigenal doublure, ventral oblique view; ×3. 5, NMV P145035; locality PL448, Borenore Limestone; pygidium and posteriormost thoracic segment, dorsal view; ×2·25. 7, NMV P144924; librigena, oblique view; ×4. 8, NMV P145038; locality PL448, Borenore Limestone; transitory pygidium with five protothoracic segments, dorsal view; ×8. 9–10, NMV P144930; transitory pygidium with three protothoracic segments and seven articulated thoracic segments, dorsal and lateral views; ×2·25. 11, NMV P144920; librigena, oblique view; ×4. 12, NMV P144943; transitory pygidium with six protothoracic segments and four articulated thoracic segments, dorsal view; ×7. 13, NMV P144932; transitory pygidium with one protothoracic segment and with last thoracic segment articulated; detail showing sculpture, oblique view; ×4. 14, NMV P144962; locality PL1995, Molong Limestone; librigena, oblique view; ×4. 15, NMV P144939; transitory pygidium with four protothoracic segments, dorsal view; ×4. 17, NMV P144938; transitory pygidium with one protothoracic segment, dorsal view; ×4. 18, NMV P144935; transitory pygidium with two protothoracic segments, latex cast in ventral view; ×2.

Figs 16, 19. *Bumastella* sp.; NMV P144972; locality PL1989, Mirrabooka Formation; pygidium, lateral and dorsal views; ×2·25.



HOLLOWAY and LANE, *Bumastella*

of Tasmania. The specimens were deposited in the former Mining and Geological Museum in Sydney, but Dr I. Percival of the Geological Survey of New South Wales has advised us that they were transferred in the 1930s to the Australian Museum, where there is now no record of their existence (Mr R. Jones, pers. comm.). Nevertheless, Etheridge's illustrations of one of the cephala clearly show that it belonged to *Bumastella*. Other specimens of *Bumastella* collected by us in the vicinity of Borenore Caves are indistinguishable from *B. spicula* from the Mirrabooka Formation and the Molong Limestone farther to the west, and we consider them to be conspecific.

A tiny pygidium from the Borenore Limestone at Borenore Caves was tentatively assigned to *Illaenus wahlenbergi* Barrande by de Koninck (1876). The small size of the specimen (3 mm long by 2 mm wide), and de Koninck's description of it as having 'four segments of the thorax ... connected to it', suggest that it may have been a meraspid. It was not illustrated and has since been destroyed by fire, so its identity is indeterminate, but the fact that it was longer than wide suggests that it did not belong to *Bumastella spicula*.

Bumastella sp.

Plate 2, figures 16, 19

Material. A single pygidium from PL1989.

Remarks. This pygidium differs from similarly sized pygidia of *Bumastella spicula*, including those from the same locality, and apparently belongs to a separate species. The differences from *B. spicula* include a more elongate outline, much lower convexity, a narrower axis anteriorly, a narrower (tr.) articulating facet and a correspondingly wider anterior pleural margin adaxial to the facet, a shallower holcos that does not extend as far backwards, finer pitting on the exterior of the exoskeleton, and several prominent ridges around the lateral and posterior margins instead of a single one. This is the only other species-group form of *Bumastella* known.

Genus BUMASTUS Murchison, 1839

Type species. By monotypy; *Bumastus Barriensis* Murchison, 1839; Barr Limestone Member of the Coalbrookdale Formation; Hay Head lime works, Great Barr, West Midlands Metropolitan County, UK.

Other species. *B. danielsi* (Miller and Gurley, 1893), *B. graftonensis* (Meek and Worthen, 1870), *B. ioxus* (Hall, 1867).

Diagnosis. See Lane and Thomas 1978*a*, p. 11.

Remarks. The taxonomic problems that effacement in trilobites has caused historically are well illustrated by this genus. Since 1839, many species of Ordovician and Silurian effaced trilobites have been referred to *Bumastus* which, until the early part of the twentieth century, was almost universally considered to be a subgenus of *Illaenus* (e.g. Barrande 1852; Burmeister 1843; Salter 1867; Holm 1886; Vogdes 1890; Weller 1907). Most of these species have since been assigned to other genera. We consider that only the three species listed above, in addition to the type species, can be assigned with confidence to *Bumastus*.

Stratigraphical range and distribution. ?Late Llandovery to earliest Ludlow; USA (Arkansas, Illinois and Oklahoma) and UK (Welsh Borderland and West Midlands).

Bumastus? sp.

Plate 4, figures 17–18

Material. A single rostral plate from PL1995.

Remarks. This rostral plate cannot be assigned to any of the other effaced styginid species known from PL1995. The specimen is tentatively assigned to *Bumastus* because it has an upwardly flexed flange posteriorly, in this respect resembling the rostral plates of *B. barriensis* (see Lane and Thomas 1978*a*, pl. 2, fig. 1b–c) and *B.* cf. *ioxus* (Hall, 1867). The rostral plates of those species differ from the present specimen, however, in that the line along which the flange is flexed upwards is strongly convex backwards rather than transverse, and the flange itself is more concave (sag.) and is smooth instead of bearing well developed terrace ridges.

Genus EXCETRA gen. nov.

Derivation of name. Latin, referring to the fanciful resemblance of the cephalon, when viewed anterolaterally, to the head of a snake; gender feminine.

Type species. Excetra iotops gen. et sp. nov.

Diagnosis. Cephalon strongly convex in transverse profile, in sagittal profile gently convex in posterior half and strongly convex in anterior half. Axial furrow subparallel to sagittal line immediately behind lunette but diverging backwards closer to posterior cephalic margin, diverging gently forwards in front of lunette and dying out just in front of glabellar midlength (sag.); omphalus and anterolateral internal pit absent. G0 large, elliptical, not reaching axial furrow, situated less than its own length from posterior margin; G1 longer (exsag.) than G0, kidney-shaped, extending close to axial furrow anteriorly; G2 comma-shaped; G3 small, transverse. Posterior fixigenal margin with well-developed articulating flange bounded anteriorly by furrow that is flexed backwards distally. Eye small, of low convexity, with posterior edge transversely opposite midlength of lunette; socle absent. Posterior branch of facial suture weakly diverging backwards; anterior branch strongly diverging. Genal angle broadly rounded. Librigenal doublure with flattened facet on posterior edge. Connective suture converging backwards across anterior part of doublure and diverging backwards across posterior part, meeting inner edge of doublure close to outer end of hypostomal suture. Rostral plate gently inflated medially; posterolaterally with acute, upwardly curved projections abaxial to strongly transversely arched hypostomal suture. Thoracic axis parallel-sided, comprising about half segmental width (tr.); articulating furrows present on axial rings; axial furrow distinct; pleurae steeply downturned abaxial to narrow (tr.), horizontal proximal portion. Pygidium moderately to strongly convex, with articulating half ring defined by well impressed articulating furrow; anteriormost pleural furrow very weakly defined adaxially, holcos absent; articulating facet rather weakly defined posteriorly.

Remarks. The cephalon of *Excetra* resembles that of *Ligiscus*, known from the type species, *L. arcanus* Lane and Owens, 1982 (p. 47, pl. 3, figs 4–8; fig. 3) from the uppermost Llandovery or lowest Wenlock of western North Greenland, and *L. smithi* Adrain, Chatterton and Blodgett, 1995 (p. 726, figs 2.1–2.2, 2.4–2.15, 3.13, 3.15–3.16) from the upper Llandovery of Alaska. The similarities include the moderate convexity of the cephalon, the axial furrow that is subparallel immediately behind the lunette and posteriorly divergent farther backwards, the absence of the omphalus, the articulating flange on the posterior cephalic margin bounded in front by a distinct furrow, the medially inflated rostral plate, and the thorax with relatively narrow (tr.), subparallel-sided axis, deep axial furrow, and articulating furrows on each of the axial rings (see Adrain *et al.* 1995). The cephalon of *Ligiscus* differs from that of *Excetra* in that the eye is much larger and is situated farther back, with its anterior edge opposite the front of the lunette; the axial furrow is more distinct in front of the lunette; G0 and G1 both extend laterally to the axial furrow, G0 is situated farther from the posterior cephalic margin and G1 is sub-quadrate rather than kidney-shaped; G2 is ovate rather than comma-shaped; the anterior branch of the facial suture is more divergent; the genal angle has a short, broad spine; the connective suture apparently converges backwards across the entire doublure instead of diverging across the posterior part; and the rostral plate apparently lacks upturned projections posterolaterally. The pygidium of *Ligiscus*, very poorly known in the type species but well documented in *L. smithi*, is not similar to that of *Excetra*, being much less convex and having a distinct axis and well-defined pleural ribs and furrows.

Excetra iotops sp. nov.

Plate 3, figures 1–19; Plate 4, figures 1–10, 13

Derivation of name. Combination of Greek 'iota' – small, and 'ops' – eye.

Holotype. Cephalon NMV P144713 (Pl. 3, figs 1–3); from PL1989.

Paratypes. Cephala NMV P144712, NMV P144717; cranidia NMV P144714–P144716, P144718, P144721, P144723–P144725, P144727, P144730, P144733; librigenae NMV P144736–P144737; rostral plates NMV P144739, P144903; incomplete thorax NMV P144751; pygidium with attached thoracic segment NMV P144731; pygidia NMV P144734, P144741–P144747, P144749–P144750, P144752, P144754; all from PL1989.

Other material. Two fragmentary cephala, five cranidia and five pygidia from PL1989.

Diagnosis. As for the genus.

Description. Cephalon *c.* 80 per cent. as long as wide (sag.) in dorsal view, widest just in front of genal angle; anterior and lateral margins uniformly curved; posterior margin of glabella gently convex backwards. Glabella gently convex (tr.) in posterior half, slightly more than half maximum width of cephalon at posterior margin, width at lunette *c.* 75 per cent. of posterior width. Median pit present on glabellar interior opposite posterior edge of G0. Lunette sub-circular, situated more than its own length from posterior edge of cephalon. Eye situated more than twice its own length from posterior cephalic margin; palpebral lobe bounded adaxially by weak furrow. Anterior and posterior branches of facial suture meeting cephalic margin approximately on same exsagittal line as palpebral suture; posterior branch with gentle sigmoidal curve; anterior branch almost straight just in front of eye, where it diverges at about 40° to sagittal axis, and broadly curved anteriorly. Posterior articulating flange strongly downturned at mid-width (tr.); articulating furrow deeper than axial furrow.

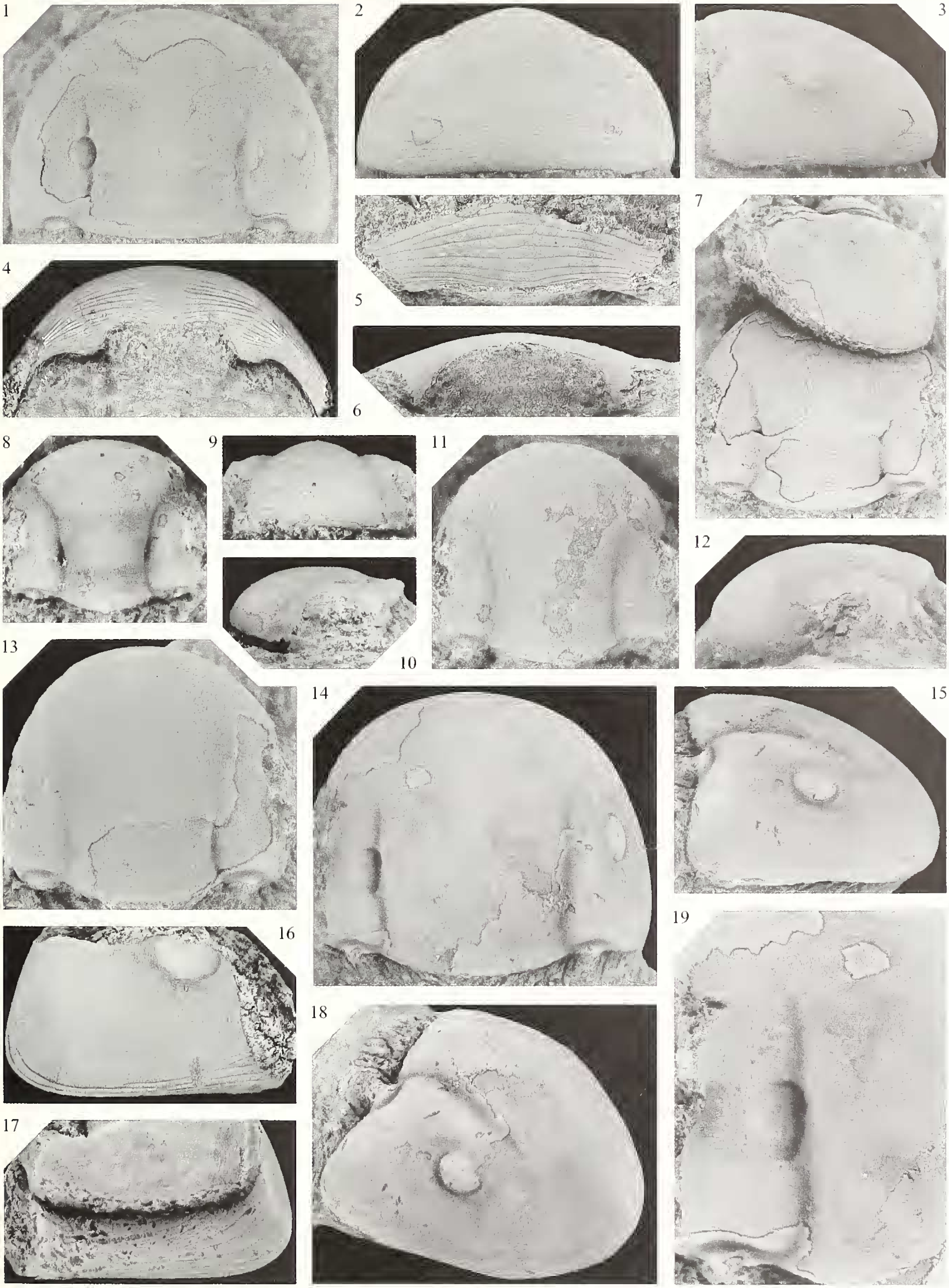
Cephalic doublure expanding and greatly increasing in convexity anteromedially towards abaxial end of hypostomal suture; facet on posterior edge of doublure not extending abaxially as far as genal angle. Median part of hypostomal suture gently arched in transverse profile, convex backwards in ventral profile; lateral part of suture deflected posterolaterally and dorsally. Narrowest (tr.) part of rostral plate situated on transverse line through median part of hypostomal suture.

Thoracic axial rings strongly arched (tr.), decreasing very slightly in length sagittally; articulating furrows short (sag., exsag.) and shallow. Inner part of pleurae (about 40 per cent. of transverse width) with very short (exsag.) articulating flange on anterior edge; outer part of pleurae gently convex (tr.), with pointed tips.

Pygidium 110–120 per cent. as wide as long (sag.) in plan view. Articulating half ring slightly less than half maximum pygidial width, gently convex (sag., exsag.). Adaxial part of anterior pleural margin with narrow (tr.)

EXPLANATION OF PLATE 3

Figs 1–19. *Excetra iotops* gen. et sp. nov.; locality PL1989, Mirrabooka Formation. 1–3, NMV P144713, holotype; cephalon, dorsal, anterior and lateral views; ×4·5. 4, NMV P144717; cephalic doublure, ventral view; ×4. 5–6, NMV P144903; rostral plate, ventral and posterior views; ×3·5. 7, NMV P144730; cranidium, palpebral view; and NMV P144731; pygidium with posteriormost thoracic segment (see Pl. 4, fig. 6), oblique view; ×4. 8–10, NMV P144727; smallest cranidium, palpebral, anterior and lateral views; ×8. 11–12, NMV P144723; cranidium, palpebral and lateral views; ×6. 13, NMV P144718; cranidium, palpebral view; ×5. 14–15, 18–19, NMV P144712; largest cephalon, palpebral, lateral and oblique views; ×3; and detail showing muscle scars on interior of glabella and fixigena; ×5. 16–17, NMV P144737; librigena, oblique dorsal and oblique ventral views; ×5.



HOLLOWAY and LANE, *Excetra*

articulating flange similar to, but weaker than, that on cephalon; abaxial to flange, anterior edge of articulating facet is weakly deflected forwards in plan view. Doublure steeply inclined, increasing slightly in width toward sagittal line where it is *c*. 40 per cent. of pygidial length in plan view; outer part of doublure gently convex, inner part gently concave and bearing about six pairs of weak radial furrows.

Sculpture. Fine, dense pits extend over external surface of cephalon and pygidium. Marginal band of subparallel terrace ridges present on anterior and lateral parts of cephalon, and curving inwards for a short distance adaxial to genal angle; this band very narrow (one to two ridges wide) posterolaterally, widest anteromedially (ten to thirteen ridges wide). Upturned part of cephalic doublure abaxial to hypostomal suture with terrace ridges more widely spaced than on narrow outer portion of doublure; terrace ridges on outer portion of doublure diverge adaxially onto rostral plate. Pygidium with terrace ridges present anterolaterally on dorsal surface, where they are largely restricted to articulating facet, running subparallel to pygidial margin on front of facet and curving posterolaterally farther back; one or two ridges extend along pygidial margin behind facet to about 75 per cent. pygidial length from anterior in plan view. Terrace ridges on outer part of pygidial doublure more closely spaced than on inner part of doublure.

Muscle scars. Glabellar muscle scars faint on external surface; on interior slightly raised (i.e. impressed on internal mould), sharply delimited and with a weak dendritic pattern on G0 and G1. G0 longer (exsag.) than wide, length equal to that of eye; G1 with posterior edge opposite front of lunette and anterior edge opposite front of axial furrow, extending closer to axial furrow anterolaterally than does G0; G2 broader abaxially than adaxially, not extending as far abaxially as G1, anterior edge at about 25 per cent. glabellar length from anterior in palpebral view; G3 close to G2 and extending farther abaxially. Interior of fixigena with numerous, small, raised scars, except on lunette (Pl. 3, fig. 9).

Pygidia with a pair of weakly impressed, sub-circular or exsagittally elongated scars (slightly raised on interior), situated either side of sagittal line a short distance behind articulating furrow (Pl. 4, fig. 5); in some specimens, these scars joined to articulating furrow by faint, anteriorly diverging furrows (Pl. 4, fig. 8). Lateral and posterolateral to these paired scars, interior of pygidium has numerous, mostly small, raised scars, some of which are arranged in six or more radial rows (Pl. 4, fig. 5) that are reflected on external surface of some specimens as extremely faint furrows; larger, radially elongated scars present towards adaxial ends of some rows (Pl. 4, fig. 9).

Ontogeny. The two smallest cranidia (sagittal length 3·3 mm in palpebral view; Pl. 3, figs 8–10) show distinct differences from the largest ones on which the preceding description is based. The differences are as follows.

1. The axial furrow is deeper, especially anteriorly where it extends almost to the cranidial margin, diverging quite strongly forwards from a point transversely opposite the front of the palpebral lobe.
2. The glabella is narrower in its posterior half (in relation to the sagittal length of the cranidium and the width across the palpebral lobes).
3. The occipital furrow is present as a shallow depression that is longer (sag., exsag.) than the occipital ring and contains muscle scar G0 laterally.
4. The occipital ring is slightly inflated medially and bears two median tubercles: a larger one on the posterior edge of the ring and a smaller one just in front.
5. G1 is more distinct on the exterior of the exoskeleton.
6. The fixigena behind the front of the palpebral lobe is not as steeply declined abaxially (compare Pl. 3, figs 2, 9).
7. There is a shallow depression on the front of the fixigena, running subparallel to and close to the anterior cephalic margin.
8. The palpebral lobe is relatively longer, the palpebral furrow is more distinct, and there is a weak eye ridge directed anteromedially from the front of the palpebral lobe.
9. The anterior and posterior branches of the facial suture diverge more strongly from either end of the palpebral lobe.
10. The lunette is larger and extends farther back, to about its own length from the posterior edge of the cephalon.

Remarks. The position of the paired muscle impressions on the anteromedian part of the pygidium of *Excetra iotops*, and the fact that in some specimens they are joined to the articulating furrow by a faint, anteriorly diverging furrow, suggest that they are homologous with the pits at the posterior end of the furrow that divides the pygidial axis longitudinally in some non-effaced styginids (see

Planiscutellum kitharos Lane and Thomas, 1978*a*, pl. 6, fig. 4b). Also probably homologous are the smooth, ovate areas on the posterolateral part of the pygidial axis of *Meroperix ataphrus*, described and illustrated by Lane (1972, p. 345, pl. 60, fig. 4b). This evidence suggests that the pygidial axis of *Excetra iotops* is very short, as in other styginids.

Genus LALAX gen. nov.

Derivation of name. Greek 'frog', alluding to the protuberant eye and palpebral area; gender masculine.

Type species. *Lalax olibros* gen. et sp. nov.

Other species. *L. bandaletovi* (Maksimova, 1975); *L. bouchardi* (Barrande, 1846) (= *Bumastus praeruptus* Kiær, 1908; see Helbert *et al.* 1982, p. 133); *L. chicagoensis* (Weller, 1907); *L. clairensis* (Thomas, 1929); *L. hornyi* (Šnajdr, 1957); *L. inflatus* (Kiær, 1908) (= *Bumastus phrix* Lane and Thomas, 1978*a*; see Helbert 1984, p. 134); *L. kattoi* (Kobayashi and Hamada, 1984); *L. lens* sp. nov.; *L. xestos* (Lane and Thomas, 1978*a*); *L.*? *sakoi* (Kobayashi and Hamada, 1984); *L.*? *transversalis* (Weller, 1907).

Diagnosis. Cephalon strongly convex (sag.), curvature in sagittal plane subtending more than 90°, height in lateral profile greater than or equal to sagittal length. Omphalus and anterolateral internal pit present. Axial furrow diverging moderately behind and immediately in front of lunette, dying out anteriorly behind omphalus. Eye large, situated less than its own length from posterior cephalic margin; socle not strongly convex (tr.). Posterior branch of facial suture strongly diverging backwards; anterior branch diverging moderately forwards. Genal angle broadly rounded. Rostral plate sub-triangular, gently convex (sag., exsag.) over anterior 70 per cent. and gently concave in posterior part, without upturned posterior flange; connective suture meeting hypostomal suture close to sagittal line; vincular furrow present across posterior edge of doublure. Thorax with very wide, gently arched axis comprising 60–70 per cent. segmental width (tr.); axial furrow weak; fulcrum situated very close to axial furrow; pleurae abaxial to fulcrum almost continuous in slope with lateral part of axial rings. Pygidium moderately convex (sag., exsag.), lenticular in dorsal view, maximum width just in front of midlength; anteriormost pleural furrow and holcos very weak or not defined. Terrace ridges present over most of dorsal surface of cephalon and pygidium.

Remarks. *Bumastus* is most easily distinguished from *Lalax* by its rostral plate that is lenticular rather than triangular in outline in ventral view and has a vertical, concave (sag.) posterior flange, and by the connective suture meeting the hypostomal suture a little farther from the sagittal line. Distinguishing the genera may be difficult in the absence of information on the rostral plate, but in *Bumastus* G0 and G1 are confluent rather than separate (compare Lane and Thomas 1983, text-fig. 2a, d); the omphalus is absent, although the anterolateral internal pit may be present; the visual surface is longer (exsag.) and narrower (tr.), with upper and lower margins parallel over almost their entire length; and the socle is more convex (tr.) and is separated from the visual surface by a deeper furrow.

In the presence of the omphalus and the anterolateral internal pit, and the outline of the rostral plate, *Lalax* is similar to *Cybantyx* (see Lane and Thomas 1978*a*, pl. 5, figs 1–8). *Cybantyx* differs from *Lalax* in having a narrow, upturned anterior and lateral cephalic border; the lunette is situated slightly farther forwards, with its anterior edge slightly in front of the anterior edge of the eye in palpebral view; the axial furrow is more distinct in front of the lunette, extending as far as the omphalus; the anterior branch of the facial suture converges weakly in front of the palpebral lobe instead of diverging; the posterior part of the rostral plate is not concave (sag.); and the pygidium is longer.

Litotix Lane and Thomas, 1978*a*, with type and only known species *L. armata* (Hall, 1865; see annotation of this reference below; Lane and Thomas 1978*a*, pl. 4, figs 8–18; text-fig. 4a–e) resembles *Lalax* in the convexity and proportions of the cephalon and pygidium, and in the presence of the omphalus. The rostral plate of *Litotix* is unknown, but the weak sagittal carina on the cephalon, the axial furrow that extends anteriorly to the omphalus, the absence of the anterolateral internal pit, and the spinose genal angle are differences from *Lalax*.

Two species are assigned to the genus with question. *L. sakoi* (see Kobayashi and Hamada 1985*b*, pl. 30, fig. 1) is known only from a cranidium, but may be synonymous with *L. kattoi* (see Kobayashi and Hamada 1985*b*, pl. 30, fig. 5), which is from the same locality and appears to differ only in its larger size; also possibly belonging to the same species is the pygidium assigned to *Bumastus glomerosus* by Kobayashi and Hamada (1987, p. 110, fig. 1A, 2.1a–d; see synonymy of *Bumastella spicula* herein). *L.*? *transversalis* is based on incomplete cephala differing from those of other species in the transverse outline and the convexity of the librigenal field; the form of the rostral plate is unknown. The only specimen of *L. clairensis* that has been figured is an internal mould of a cranidium (Thomas 1929, pl. 1, fig. 6), but one of us (DJH) has studied additional material, including librigenae and an incomplete cephalon with part of a rostral plate, allowing confident assignment of the species to *Lalax*. Also assigned here to *Lalax* are the specimens from the Estonian islands of Saaremaa and Muhu figured by Holm (1886, p. 164, pl. 11, figs 12–16) as '*Illaenus*' *barriensis*.

Stratigraphical range and distribution. ?Late Llandovery (or early Wenlock) to Ludlow; eastern USA, UK (Welsh Borders), southern Norway, Estonia, Bohemia, Kazakhstan, Japan and New South Wales.

Lalax olibros sp. nov.

Plate 4, figures 11–12, 14–16, 19–20; Plate 5, figures 1–23;
Plate 6, figures 9, 13, 16, 18

Derivation of name. Greek 'slippery', referring to the smooth, effaced appearance of the exoskeleton.

Holotype. Pygidium NMV P144800, Pl. 6, figs 9, 13, 16, 18; from PL1993.

Paratypes. From PL1993: cephala NMV P144758–P144760, P144762–P144763; cranidia NMV P144765–P144767, P144770, P144772; cranidium with incomplete thorax NMV P144771; librigenae NMV P144780–P144785, P144788–P144790; rostral plates NMV P144792–P144794; hypostome NMV P144796; incomplete thorax NMV P145048; pygidia (including meraspid transitory pygidia) NMV P144773, P144797, P144801–P144804, P144806–P144808, P144810. From PL1991: cephalon NMV P144819; cranidium P144817; pygidium with incomplete thorax NMV P144822. From PL1998: cranidium NMV P144811; librigena NMV

EXPLANATION OF PLATE 4

Figs 1–10, 13. *Excetra iotops* gen. et sp. nov.; locality PL1989, Mirrabooka Formation. 1–2, 4, NMV P144746; pygidium, dorsal, lateral and anterodorsal views; ×4·5. 3, NMV P144751; incomplete thorax, dorsal view; ×7. 5, NMV P144747; pygidium, dorsal view; ×4. 6, NMV P144731; pygidium with posteriormost thoracic segment articulated, dorsal view; ×5. 7, 10, 13, NMV P144743; pygidium with dorsal surface excavated to expose external mould of doublure, dorsal, posterior and lateral views; ×3·25. 8, NMV P144744; pygidium, detail to show weak longitudinal furrows connecting paired muscle scars to articulating furrow, dorsal view; ×5·5. 9, NMV P144741; pygidium, detail showing muscle scars arranged in longitudinal rows on interior of exoskeleton, dorsal view; ×5.

Figs 11–12, 14–16, 19–20. *Lalax olibros* gen. et sp. nov.; Mirrabooka Formation; locality PL1993 unless otherwise indicated. 11, NMV P144812; locality PL1998; librigena, oblique view; ×5. 12, NMV P144780; librigena, latex cast, ventral oblique view; ×4. 14, NMV P144789; librigena, oblique view; ×7. 15, NMV P144782; librigena, oblique view; ×4. 16, NMV P144796; hypostome, latex cast in ventral view; ×5. 19, NMV P144771; cranidium with three articulated thoracic segments, dorsal view; ×3. 20, NMV P145048; incomplete thorax, dorsal view; ×4.

Figs 17–18. *Bumastus*? sp.; locality PL1995, Molong Limestone; NMV P145047; rostral plate, ventral and posteroventral views; ×4.

HOLLOWAY and LANE, *Excetra*, *Lalax*, *Bumastus*?

P144812; pygidia (including meraspid transitory pygidia) NMV P144813–P144814, P144816, P144944. From PL3301: cranidium NMV P145052; pygidium NMV P145049. From PL3303: cranidium NMV P145051.

Other material. Five cephala, 14 cranidia, five librigenae, a rostral plate, a pygidium with incomplete thorax and seven pygidia from PL1993, PL1991, PL1995 and PL3303.

Diagnosis. Cranidium *c.* 130 per cent. as wide across palpebral lobes as long (sag.) in palpebral view. Axial furrow almost indistinguishable behind lunette; latter situated with posterior edge just in front of posterior edge of palpebral lobe. Anterolateral internal pit lying slightly adaxial to exsagittal line through omphalus. Connective suture subtending angle of *c.* 105° at back of rostral plate. Pygidium strongly convex, more so in posterior than in anterior half; anteriormost pleural furrow and holcos not defined. Terrace ridges confined to anterior, lateral and posterior margins of cephalon, posterior part of librigenal field, and anterior margin of pygidium. Cranidial muscle impressions indistinguishable.

Description. Cephalon convex, in lateral view sagittal profile describing an arc of *c.* 120°, in anterior view transverse profile rather less that semicircular; in palpebral view sagittal length 70 per cent. of maximum transverse width, which is level with posterior half of palpebral lobe. Axial furrow barely discernible posterior to very weakly impressed lunette, not defined in front of lunette. Interior of cephalon with median pit (forming median node on internal moulds) about half way between posterior margin and transverse line through back of lunette. Palpebral lobe indicated in anterior view by slight upward break in slope from uniform transverse convexity of glabella and adjacent fixigena; in palpebral view, palpebral lobe about 40 per cent. of sagittal length of cephalon, situated about 60 per cent. of its own length from posterior cephalic margin. Anterior section of facial suture gently sigmoidal, diverging slightly forwards from front of palpebral lobe, converging fairly strongly anteriorly in a broad arc to meet rostral suture more-or-less on an exsagittal line through anterolateral internal pit; posterior section of suture short, weakly sigmoidal, directed posterolaterally at an angle of *c.* 30° to transverse direction. Librigena convex (exsag., tr.), steeply inclined, slightly overhanging lateral margin; genal angle broadly rounded. Visual surface gently convex dorsoventrally, in dorsal view almost paralleling curvature of lateral margin of librigena; lenses (visible only as impression on internal moulds) tiny, increasing slightly in size towards top of eye. Socle highest at midlength, weakly convex (tr.) except anteriorly where it dies out into broad, shallow furrow at front of eye.

Rostral plate 40 per cent. as long (sag.) as maximum width (tr.); width across hypostomal suture *c.* 10 per cent. maximum width; rostral suture gently convex forwards; connective sutures weakly convex outwards in anterior half and weakly concave outwards in posterior half. Abaxial to rostral plate, doublure decreases in convexity posteriorly; vincular furrow well rounded in cross section.

Hypostome about twice as wide across anterior wings as long (sag.); lateral margin almost straight and converging strongly backwards between anterior and posterior wings; posterior margin rounded. Maculae

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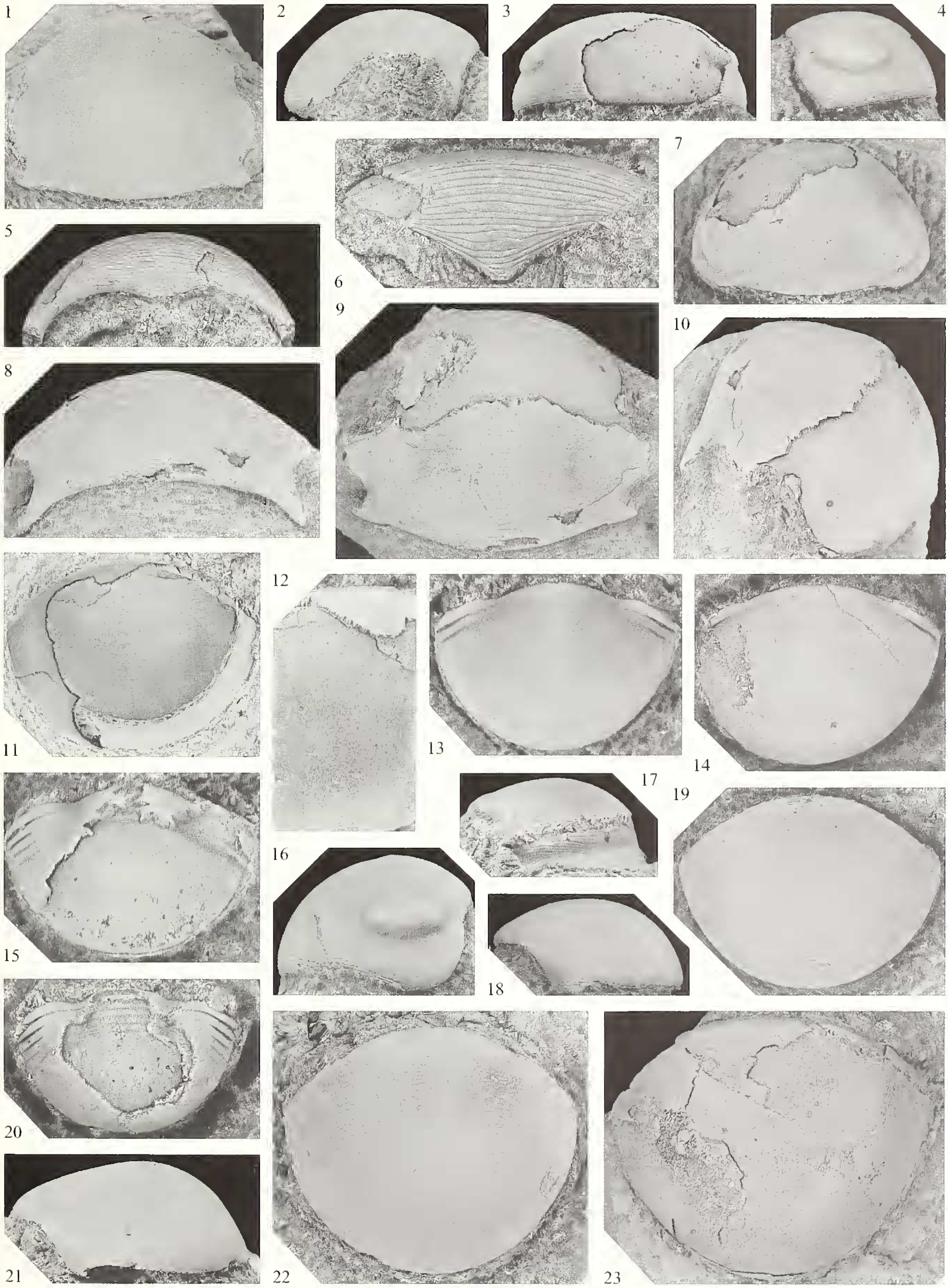
EXPLANATION OF PLATE 5

Figs 1–23. *Lalax olibros* gen. et sp. nov.; Mirrabooka Formation unless otherwise indicated. 1–2, NMV P144817; locality PL1991; cranidium, palpebral and lateral views; ×2·5. 3–4, 7, NMV P144762; locality PL1993; small cephalon, anterior, lateral and palpebral views; ×4·5. 5, NMV P144819; locality PL1991; cephalic doublure, ventral view; ×3. 6, NMV P144793; locality PL1993; rostral plate, ventral view; ×4. 8–10, NMV P144766; locality PL1993; largest cranidium, posterodorsal, palpebral and oblique views; ×2. 11–12, 17, NMV P144813; locality PL1998; pygidium, latex cast in ventral view; ×2·5; detail of internal mould showing muscle scars; ×4; internal mould, lateral view; ×2·5. 13, NMV P144808; locality PL1993; transitory pygidium with two protothoracic segments, dorsal view; ×6. 14, NMV P144806; locality PL1993; transitory pygidium with one protothoracic segment, dorsal view; ×4·5. 15, NMV P144810; locality PL1993; transitory pygidium with four protothoracic segments, dorsal view; ×8. 16, NMV P144760; locality PL1993; cephalon, lateral view; ×3. 18–19, NMV P144802; locality PL1993; pygidium, lateral and dorsal views; ×3. 20, NMV P144944; locality PL1998; smallest transitory pygidium, with five protothoracic segments, dorsal view; ×8. 21–22, NMV P145049; locality PL3301, Borenore Limestone; pygidium, lateral and dorsal views; ×2. 23, NMV P144797; locality PL1993; pygidium, dorsal view; ×1·75.



HOLLOWAY and LANE, *Lalax*

inflated, situated at about 60 per cent. of hypostomal length (sag.) from anterior; middle furrow shallow abaxially, not impressed medially. Anterior lobe of middle body sub-trapezoidal, strongly convex transversely and weakly convex sagittally, sloping fairly steeply backwards; posterior lobe of middle body crescentic, moderately convex transversely and gently concave sagittally. Lateral and posterior borders narrow, rounded in section; border furrows shallow.

Thoracic axis narrowing gently backwards, comprising 60–65 per cent. of total segmental width (tr.); pleurae successively more weakly flexed backwards at fulcrum from front to back of thorax; anterior edge of segments with wide (tr.) articulating flange at inner end of facet.

Pygidium ovate; in plan view length (sag.) 75 per cent. of maximum width, which is situated in front of midlength. Anterior margin gently arched forwards between fulcra, distance between fulcra *c*. 65 per cent. maximum pygidial width; articulating facet short (exsag.), with panderian protuberance on anterior edge at *c*. 40 per cent. distance from abaxial to adaxial extremities of facet. Posterior pygidial margin broadly rounded. Doublure convex, steeply inclined, occupying *c*. 15 per cent. of sagittal length of pygidium in plan view, narrowing forwards a little and increasing in convexity near anterolateral extremity of pygidium.

Sculpture. Dorsal surface of cephalon and pygidium covered with fine pits, except on lunette and visual surface of eye; these pits are external openings of perforations that are surrounded on interior of exoskeleton by raised rims (visible on internal moulds as tiny pits *c*. 0·1 mm in diameter). Anterior and posterior parts of cranidium with terrace ridges running subparallel to cephalic margins; terrace ridges on posterior part of librigenal field weakly sinuous, anastomosing and running subparallel to base of eye, dying out on anterior part of librigenal field. Terrace ridges on cephalic margins, rostral plate and strongly convex outer part of librigenal doublure are higher, more closely spaced and more continuous than on dorsal surface and on steeply inclined inner part of librigenal doublure; narrow (sag., exsag.) band devoid of terrace ridges present across front of rostral plate (Pl. 5, fig. 6); on posterior part of librigenal doublure, terrace ridges do not extend behind anterior slope of vincular furrow. Terrace ridges on front of pygidium running subparallel to anterior margin, most closely spaced laterally on and just behind articulating facet, deflected backwards at lateral pygidial margin. On pygidial doublure terrace ridges run concentrically, except anterolaterally where they gently curve abaxially across doublure. Interior of pygidium with a narrow, slightly impressed (slightly raised on internal mould) sagittal band extending over posterior half of pygidium; this sagittal band is devoid of openings of exoskeletal perforations.

Muscle scars. A pygidium of moderate size (maximum width 16·3 mm) has a pair of small, circular muscle scars, situated close to sagittal line opposite maximum pygidial width in plan view (Pl. 5, figs 11–12); these scars are slightly raised on interior of exoskeleton (weakly impressed on internal mould). Adjacent to these scars posterolaterally there may be a pair of larger, extremely weak sub-circular scars.

The two smallest meraspid transitory pygidia have a pair of elliptical or ovate muscle scars gently impressed on the interior of the exoskeleton (slightly raised on internal mould) opposite the lateral extremity of the future pygidium (Pl. 5, figs 15, 20). Between the scars, and extending forwards to the front of the future pygidium, is a conical, slightly raised (on internal mould) area, probably representing at least in part the axis. Similar scars are present in pygidia of *L. bouchardi* (see Šnajdr 1957, pl. 11, fig. 11) and *L. inflatus* (= *Bumastus phrix*) of Lane and Thomas (1978*a*, pl. 3, figs 3, 10).

Ontogeny. The progressive decrease in the number of protothoracic segments with increasing size of meraspid transitory pygidia has been outlined above in the section on segmental variation. Other morphological changes occurring during ontogeny include the following.

1. A slight node is present on the genal angle in the smallest cephala and librigenae (Pl. 4, fig. 14; Pl. 5, fig. 4) but is lost in larger specimens.

2. The eye decreases in size relative to the sagittal length of the cephalon, and the librigenal field correspondingly increases in width (compare Pl. 4, figs 14–15).

Remarks. Of previously described species of this genus, the best known are *L. bouchardi* from the Wenlock of Bohemia (Šnajdr 1957, p. 109, pl. 10, figs 1–9, pl. 11, figs 1–13) and the Oslo Region, Norway (Whittard 1939, p. 287, pl. 3, figs 1–4), and *L. inflatus* from the Wenlock of Norway (Whittard 1939, p. 289, pl. 3, figs 5–8) and the Welsh Borderlands (Lane and Thomas 1978*a*, p. 14, pl. 3, figs 1–22). Both of these species differ from *L. olibros* in having terrace ridges more widely distributed on the cephalon and pygidium, and forming a concentric elliptical pattern on the librigenal field; and in having a less convex pygidium with weak but distinct anteriormost pleural furrow and holcos. Examination of type and other specimens of *L. bouchardi* shows that this species also differs from *L. olibros* in having a more distinct cephalic axial furrow; the palpebral lobe is situated closer to the posterior cephalic margin and the cranidium in front of the palpebral lobe is relatively longer; there is a short (sag., exsag.), slightly convex border on the anterior and lateral cephalic margins; and the anterior section of the facial suture is straighter. *Lalax inflatus* also differs from *L. olibros* in having the anterolateral internal pit situated closer to the omphalus and slightly abaxial rather than adaxial to it; the eye socle is more convex posteriorly where it is separated from the visual surface by a deeper furrow; and the terrace ridges on the librigenal doublure extend farther posteriorly, across the vincular furrow.

Šnajdr (1957, pl. 10, figs 10–11) illustrated only a pygidium and an incomplete cranidium of *Lalax hornyi*, from the Ludlow of Bohemia, but an articulated dorsal exoskeleton (see Barrande 1872, pl. 16, figs 15–18; Šnajdr 1990, p. 147) from a similar horizon at a different locality was assigned to this species by Marek (*in* Horný and Bastl 1970, p. 83). This specimen differs from *L. olibros* in having terrace ridges arranged in a concentric ellipse on the librigenal field, a deeper furrow below the eye socle, the anterolateral internal pit (visible on exterior of exoskeleton) situated anterolateral to the omphalus instead of anteromedial to it, a less convex pygidium with a distinct holcos, terrace ridges covering almost the entire dorsal surface of the pygidium, and a weak sagittal ridge on the posterior half of the pygidium.

The smallest meraspid transitory pygidia of *Lalax olibros* and *Bumastella spicula* are exceedingly alike (compare Pl. 2, fig. 8 and Pl. 5, fig. 20). The specimen of *B. spicula* is distinguished by its much weaker convexity and very weakly developed anteriormost pleural furrow on the future pygidium.

Lalax lens sp. nov.

Plate 6, figures 1–8, 10–12, 14–15, 17, 19–20

Derivation of name. Greek 'lens', referring to the similarity of the outline of the pygidium to a biconvex lens.

Holotype. Cranidium NMV P144824 (Pl. 6, figs 1–3); from PL1989.

Paratypes. Cranidia NMV P144823, P144825–P144826; librigenae NMV P144827–P144829; rostral plates NMV P144831–P144832; pygidia with incomplete thoraces NMV P144836–P144837; pygidia NMV P144833–P144835, P144929, P145046; all from PL1989.

Diagnosis. Cranidium *c*. 110 per cent. as wide across palpebral lobes as long (sag.) in palpebral view. Axial furrow shallow but distinct behind lunette; latter situated with posterior edge well in front of posterior edge of palpebral lobe. Connective suture subtending angle of *c*. 145° at back of rostral plate. Pygidium evenly convex in sagittal profile. Terrace ridges present over entire dorsal surface of pygidium, and all of cephalon except for median part of cranidium between front of palpebral lobe and posterior edge of lunette.

Description. The description of *L. olibros* applies also to *L. lens*, except for details of muscle scars and the differences listed below in the remarks.

Muscle scars. These are most easily seen in largest cranidium (Pl. 6, fig. 4), in which they are weakly impressed and also defined by fine wrinkling or reticulate ridging of external surface, although edges of scars are poorly defined. G0 largest, sub-circular, situated midway between sagittal line and axial furrow, and less than its own length from posterior cephalic margin; anterior edge of scar opposite back of palpebral lobe in palpebral view. G1 situated slightly closer to sagittal line than G0, elongated exsagittally, in palpebral view with posterior edge level with narrowest part of glabella and anterior edge opposite or just behind front of palpebral lobe. G2 and G3 sub-circular; G2 situated same distance from sagittal line as G0 and at *c*. 38 per cent. of cephalic length from anterior in palpebral view; G3 slightly larger than G2, situated farthest from sagittal line, and in front of transverse line through omphalus in palpebral view.

Remarks. *L. lens* differs from *L. olibros* in the following.

1. The cranidium is relatively longer, especially in front of the palpebral lobe. In plan view, the anterior edge of the palpebral lobe is situated almost opposite the cephalic midlength (sag.) in *L. lens* but in front of the midlength in *L. olibros*.
2. The lunette is situated slightly farther forwards, with its posterior edge well in front of the back of the palpebral lobe, whereas in *L. olibros* the posterior edge of the lunette is almost level with the back of the palpebral lobe (compare Pl. 6, fig. 1 and Pl. 5, fig. 9).
3. The rostral plate is less acute in outline posteromedially (compare Pl. 6, fig. 17 and Pl. 5, fig. 6).
4. The pygidium is distinctly less convex (sag., exsag., tr.; compare Pl. 6, figs 9–11, 13).
5. Terrace ridges are more widely distributed on the exoskeleton. On the cranidium they extend from the anterior margin backwards almost to the front of the palpebral lobe, from the posterior margin as far forwards as the posterior edge of the lunette, and over most of the palpebral area. On the librigena terrace ridges cover most of the field and are separated from longer, straighter, more prominent and more closely spaced ridges on the lateral margin by a narrow groove that gradually converges with the librigenal margin towards the genal angle and becomes deeper; adaxial to the genal angle, this groove is crossed by several prominent, forwardly deflected terrace ridges and dies out. Terrace ridges are present over the entire dorsal surface of the pygidium.

Genus RHAXEROS Lane and Thomas, 1980

Type species. *Rhax pollinctrix* Lane and Thomas, 1978*b* from the Quinton Formation (Upper Llandovery) of northern Queensland.

Other species. *R. latus* (Chatterton and Campbell, 1980); *R. subquadratus* (Kobayashi and Hamada, 1974); *R. synaimon* sp. nov.; *R. trogodes* sp. nov; *R.*? *shinoharai* (Kobayashi and Hamada, 1974).

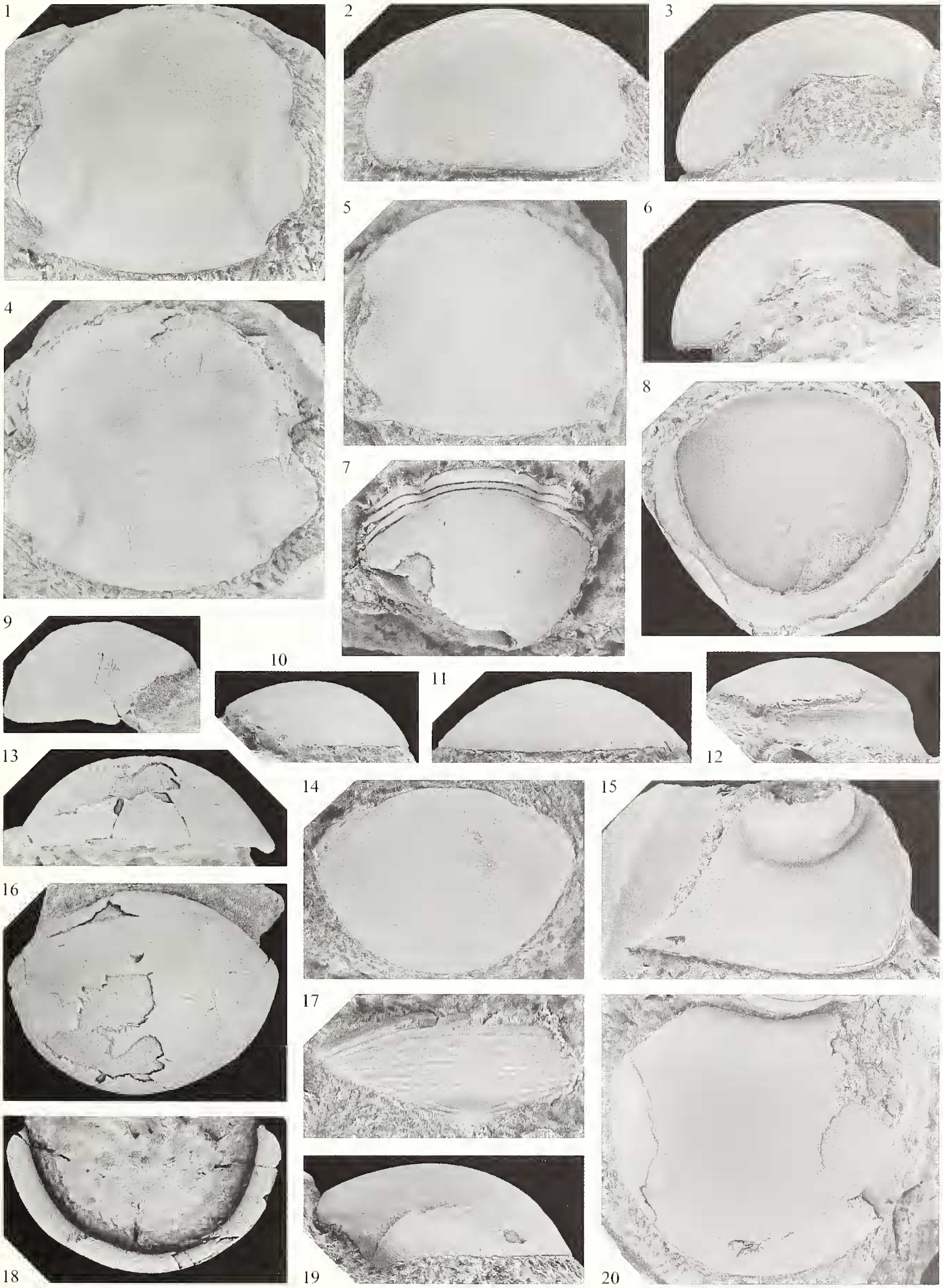
Diagnosis. Cephalon gently convex (sag., tr.); axial furrow converging anteriorly and posteriorly towards lunette, joining posterior border furrow in a curve; preglabellar and lateral border furrows may be weakly defined. Omphalus and anterolateral internal pit absent. Librigena with posterior margin slightly concave in outline and genal angle rounded or subangular; eye small to large, with bean-shaped visual surface; socle absent. Rostral plate lenticular in outline, without upturned posterior flange, gently transversely arched just in front of hypostomal suture; connective suture meeting hypostomal suture rather far from sagittal line. Librigenal doublure with fan-shaped vincular depression posterolaterally, just in front of flattened, triangular facet on posterior margin. Hypostome about twice as wide across anterior wings as long (sag.), with subangular shoulder and posterior margin strongly rounded in outline; middle furrow deep abaxially; macula inflated. Thorax with evenly arched axis comprising 60–70 per cent. segmental width (tr.), and with pleurae

EXPLANATION OF PLATE 6

Figs 1–8, 10–12, 14–15, 17, 19–20. *Lalax lens* sp. nov.; locality PL1989, Mirrabooka Formation. 1–3, NMV P144824, holotype; cranidium, palpebral, anterior and lateral views; × 1·75. 4, NMV P144823; largest cranidium, palpebral view; × 1·5. 5–6, NMV P144825; cranidium, palpebral and lateral views; × 3. 7, NMV P144836; transitory pygidium with one protothoracic segment incompletely separated and two thoracic segments articulated, dorsal view; × 5. 8, 12, NMV P145046; pygidium, latex cast in ventral view and internal mould in lateral view; × 1·75. 10–11, 14, NMV P144833; pygidium, lateral, posterior and dorsal views; × 3. 15, NMV P144828; librigena, oblique view; × 2·5. 17, NMV P144832; rostral plate, ventral view; × 4. 19–20, NMV P144929; largest pygidium, lateral and dorsal views; × 1·5.

Figs 9, 13, 16, 18. *Lalax olibros* gen. et sp. nov.; NMV P144800, holotype; locality PL1993, Mirrabooka Formation; pygidium, lateral, posterior, dorsal and ventral views; × 2·25.

PLATE 6



HOLLOWAY and LANE, *Lalax*

strongly downturned abaxial to very narrow (tr.) articulated portion; first segment longer (sag., exsag.) than remainder, with axial ring expanding strongly backwards and with articulating furrow impressed; articulating furrow very weak or absent on more posterior segments. Pygidium more convex than cephalon, a little wider than long, commonly with weak, radially disposed ribs and furrows laterally; holcos weak to absent.

Remarks. Lane and Thomas (1980, p. 191) proposed *Rhaxeros* as the replacement name for *Rhax* Lane and Thomas, 1978*b* (*non* Hermann, 1804).

Failleana Chatterton and Ludvigsen, 1976, resembles *Rhaxeros* in many features, including the convexity of the cephalon, the course of the axial furrow, the size and position of the eye, the shape of the rostral plate, the thorax with a very broad axis and very narrow (tr.) articulated portion of the pleurae, and the pygidium with holcos weak or absent. *Failleana* is distinguished from *Rhaxeros* mainly by the presence of the omphalus, a character to which we attribute considerable taxonomic importance.

Leioscutellum Wu, 1977 closely resembles *Rhaxeros* in the glabella that expands strongly backwards close to the posterior margin, the very large eye, the rounded genal angle, the weak lateral border furrow on the librigena, the shape and convexity of the pygidium, the weak radial ribs and furrows on the lateral part of the pygidium, and the very shallow holcos. The type and only known species, *L. tenuicaudatus* Wu, 1977, (p. 98, pl. 1, figs 1–2; text-fig. 4.1a–b) from the upper Llandovery (Telychian) of south-west China, apparently differs from *Rhaxeros* species in having a distinct occipital furrow, but comparison of cephalic characters is hindered by the fact that the material of *L. tenuicaudatus* lacks the anterior part of the cephalon. *Leioscutellum* may yet be shown to be a senior synonym of *Rhaxeros*, but until *L. tenuicaudatus* becomes better known we believe that *Leioscutellum* should be restricted to the type material.

Goldillaenus shinoharai Kobayashi and Hamada, 1974 (p. 53, pl. 3, fig. 6, text-fig. 2G) is based on a single cranidium that resembles *Rhaxeros* in the moderate convexity and the course of the axial furrow, but the illustration of the specimen does not allow further assessment. Pending revision of the species, we assign it to *Rhaxeros* with question.

Stratigraphical range and distribution. Late Llandovery to ?early Ludlow; Queensland, New South Wales, Australian Capital Territory and Japan.

Rhaxeros synaimon sp. nov.

Plate 7, figures 1–21; Plate 8, figures 18–19

Derivation of name. Greek 'kinsman' referring to its relationship with the type species.

Holotype. Cranidium NMV P144847 (Pl. 7, figs 8, 11–12); from PL1989.

Paratypes. Cephala NMV P144845–P144846, P144863; cranidium with rostral plate NMV P144860; cranidium with anteriormost thoracic segment NMV P144890; cranidia NMV P144848–P144851, NMV P144853–P144859, P144861–P144862; librigenae NMV P144865–P144870, P144917; rostral plate NMV P144892; thoracic segments NMV P144735, P144872–P144875, P144893; pygidia NMV P144876–P144881, P144883–P144884, P144887–P144889; all from PL1989.

Other material. Eight cranidia, two librigenae, a rostral plate, two thoracic segments and three pygidia from PL1989, PL1991, PL1992, PL1993, PL1995 and PL1998.

Diagnosis. Axial furrow dying out anteriorly in front of lunette; preglabellar and anterior border furrows not defined; lateral border furrow very weak on librigena. Eye less than half maximum length of librigena, gently curved in dorsal view, its anterior edge level with front of lunette. Posterior section of facial suture meeting posterior cephalic margin in line (exsag.) with its origin at posterior of visual surface; connective suture evenly curved, meeting rostral suture at an acute angle. Pygidium with shallow holcos and up to four, weakly defined pleural ribs and furrows. Sculpture of distinct, small pits present over most of dorsal surface; terrace ridges on cranidium restricted to narrow band anteriorly; pygidium with terrace ridges on and just behind articulating facet, and close to lateral and posterior margins.

Description. Cephalon gently convex in sagittal line, with maximum curvature anteriorly, describing less than a semicircle transversely; in palpebral view sagittal length almost 65 per cent. of maximum transverse width, which is situated just in front of genal angle and level with posterior edge of eye. Axial furrow clearly impressed posterior to lunette, diverging gently backwards, very weak behind junction with distinct posterior border furrow that runs slightly obliquely forward abaxially on fixigena. Axial furrow less distinct in front of lunette than behind, diverging at *c.* 40° to sagittal axis, dying out as an obvious feature at about 60 per cent. of cephalic length from posterior margin and close to anterior section of facial suture. Small, weak median glabellar (occipital) node present on both exterior of exoskeleton and internal mould opposite posterior edge of eye. Lunette ovate, width (tr.) *c.* 60 per cent. maximum length (which is slightly oblique to an exsagittal line), adaxial margin more distinct than abaxial, especially on internal mould. Palpebral lobe *c.* 25 per cent. sagittal length of cephalon, placed less than 50 per cent. of its length from posterior cephalic margin. Palpebral furrow broad, very weak, running subparallel to palpebral rim. Palpebral area very gently inflated. Anterior section of facial suture gently convex adaxially immediately in front of palpebral lobe, thereafter almost straight and diverging at *c.* 20° to sagittal line, near anterior margin strongly curved adaxially. Posterior section of suture very short, curved abaxially and then adaxially.

Lateral margin of librigena gently curved, meeting gently concave-forwards posterior margin at sharply rounded genal angle. Lateral border furrow broad and weak, running about mid-way between base of eye and lateral margin, dying out anteriorly against facial suture, extending close to cephalic margin posteriorly where it joins in strong curve with equally weak librigenal portion of posterior border furrow (Pl. 7, fig. 15). Visual surface bounded below by a distinct furrow which is narrowest at midlength of eye, widest anteriorly, and confluent with posterior border furrow behind eye. Lenses visible on external surface of eye, increasing in size towards top of visual surface. Librigenal doublure gently convex (tr.) anteriorly, increasing greatly in width at outer end of hypostomal suture due to dorsal deflection of inner margin; posterolateral to this expansion, outer part of doublure gradually decreases in convexity and inner part becomes gently concave. Rostral plate more convex exsagittally than sagittally due to transverse arching of hypostomal suture; connective suture converging at *c.* 65° to sagittal line.

Thorax incompletely known but similar to that of *R. trogodes*.

Pygidium *c.* 75 per cent. as long as wide in plan view, more convex transversely than sagittally, lateral and posterior margins with greatest curvature medially. Articulating half ring marked by very indistinct articulating furrow (Pl. 7, fig. 21), indicating anterior width of axis which is 60 per cent. maximum pygidial width. Abaxial extremity of articulating half ring separated from adaxial extremity of articulating facet by only a very narrow section of anterior pleural margin that is almost horizontal in anterior profile and has the appearance of a shallow notch in dorsal profile (Pl. 7, figs 6, 21). Posterior edge of articulating facet marked adaxially by most anterior and most distinct of up to four pleural ribs; facet not as clearly differentiated abaxially from shallow holcos situated adjacent to lateral and posterior margins. Doublure in plan view about 20 per cent. of maximum pygidial width anterolaterally, posteriorly somewhat less than 50 per cent. sagittal length. Outer portion (about 30 per cent.) of doublure gently convex, inner portion weakly concave; inner portion bears a sagittal ridge which is widest and most distinct anteriorly.

Sculpture. Dense pits covering most of dorsal exoskeleton are absent on lunette, rim of palpebral lobe adjacent to palpebral suture, posterior to eye on cranidium and librigena, in a narrow band across front of thoracic segments and pygidium, and on articulating facets of thorax and pygidium. Terrace ridges on front of cephalon run parallel to anterior margin, becoming discontinuous and more sinuous posteriorly; abaxially, they increase in height and become restricted to cephalic margin, only a single, prominent ridge extending backwards along lateral librigenal margin as far as genal angle (Pl. 7, fig. 15). Pygidium with terrace ridges on articulating facet and anteriormost pleural rib, short oblique ones close to lateral margin, and a few close to and subparallel to posterior margin. Terrace ridges on cephalic and pygidial doublure higher and more continuous than on dorsal surface, closely spaced on rostral plate, widely spaced on inner part of librigenal doublure.

Muscle scars. G0 sub-circular, slightly inflated on exterior of exoskeleton, placed at its own diameter from posterior margin and nearer to axial furrow than to sagittal line, its anterior margin just behind transverse line through posterior edge of lunette. G1 sub-circular or sub-triangular, slightly larger than G0, placed well forward with its posterior margin about opposite anterior edge of lunette. G2 sub-circular, a little smaller than G1 and placed close to it at about 30 per cent. cephalic length (sag.) from anterior. G3 small, transversely elliptical, situated immediately in front of G2 and lateral to it. Small, accessory muscle scar possibly present between G0 and G1. Internal surface of palpebral area with numerous small, sub-circular, raised scars (impressed on internal moulds).

Remarks. The largest cranidium (the holotype; Pl. 7, figs 8, 11–12) and an incomplete cephalon of similar size have a weak sagittal carina running forward from a point opposite the lunette. In the holotype, the carina swells anteriorly into an elongated oval feature which terminates near the posterior edge of the zone of terrace ridges. The most complete known thorax of *Rhaxeros synaimon* consists of five segments (Pl. 7, fig. 19); comparison with *R. trogodes* (see below) indicates that these are the first five thoracic segments (anteriormost segment longer (sag., exsag.) than remainder, with strongly backwardly expanding axial ring, with large anterior articulating flange at fulcrum, and with strongly backwardly deflected articulating facet).

Many detailed characters serve to distinguish *Rhaxeros synaimon* from the type species. In general, *R. pollinctrix* is not as effaced, having very shallow preglabellar and anterior border furrows on the abaxial part of the cranidium, a cephalic axial furrow that does not die out anteriorly, and better developed pygidial pleural ribs and furrows, especially in smaller specimens; in *R. synaimon* pleural ribs and furrows are not discernible in small pygidia although they are very weakly indicated in large ones. *R. pollinctrix* also differs in that the glabella narrows more strongly forwards towards the lunette; the lunette is situated slightly farther backwards opposite the midlength (exsag.) of the palpebral lobe; the eye is proportionately larger and much more convex in both anterior and palpebral views; the posterior border furrow is weaker on the fixigena; the posterior branch of the facial suture is more divergent; and the cephalon and pygidium have more extensive terrace ridges dorsally but lack dense pitting.

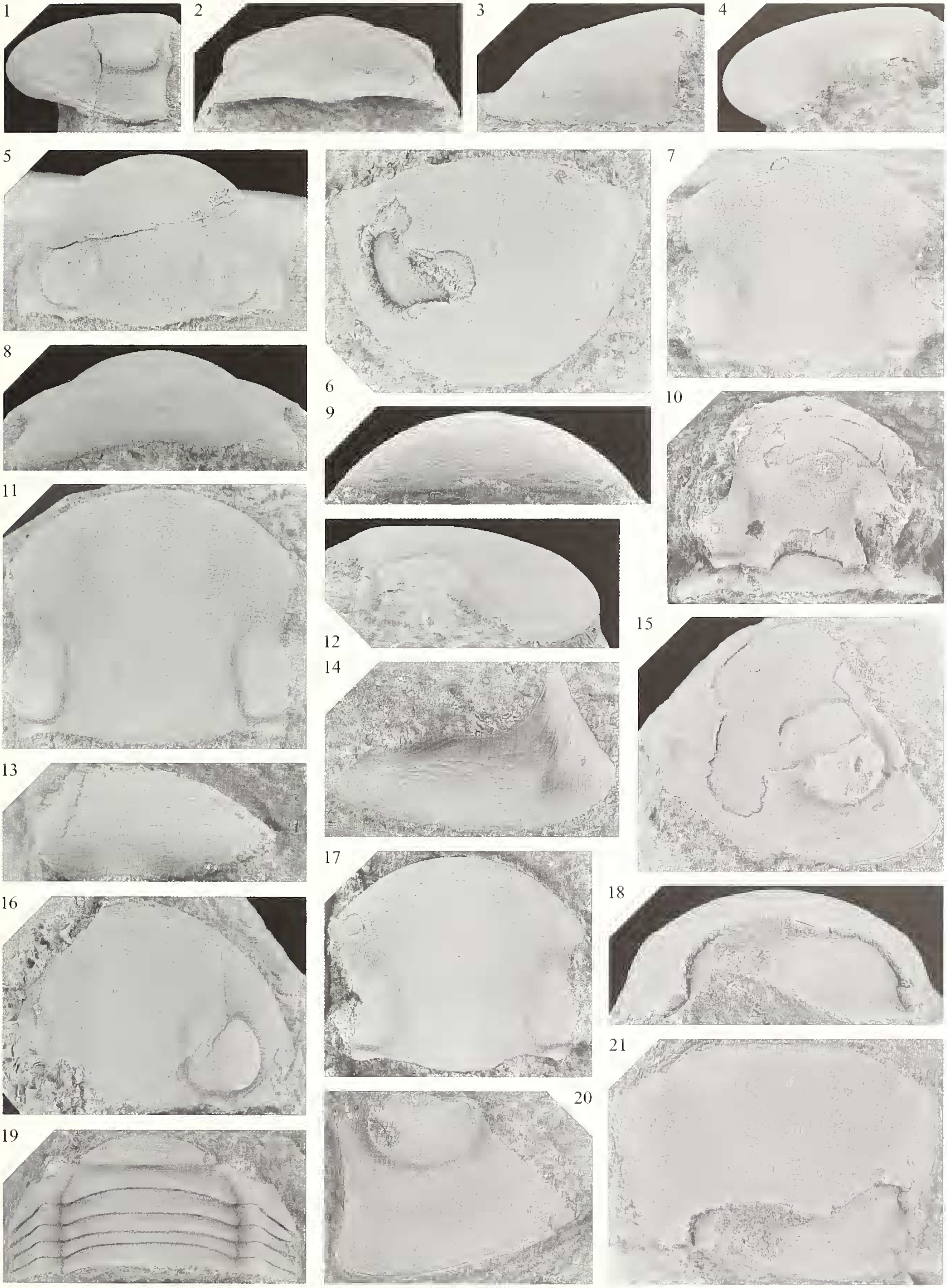
Goldillaenus? *latus* Chatterton and Campbell, 1980 (p. 83, pl. 7, figs 7–9, 11–21) from the Walker Volcanics (Wenlock) near Canberra is here assigned to *Rhaxeros*. It differs from *R. synaimon* in that the cephalic axial furrow diverges more strongly backwards behind the lunette, the palpebral lobe is more strongly curved in outline, the posterior branch of the facial suture diverges strongly backwards, and the pygidium lacks a distinct holcos. In addition, the pygidium of *R. latus* appears to lack weak radial ribs and furrows laterally, although this may be due to the relatively poor preservation of the material.

Examination of a cast of the pygidium figured by Kobayashi and Hamada (1974, pl. 3, fig. 6a–c) as *Bumastus* (*Bumastella*) *aspera* shows that it does not belong to *Bumastella* but to *Rhaxeros*, and closely resembles or is possibly conspecific with *R. synaimon*. The similarities with *R. synaimon* include the convexity, the shallow holcos, the very weak radial ribs anterolaterally, the dense sculpture of fine pits, and the distribution of terrace ridges on the first rib and close to the lateral margin.

EXPLANATION OF PLATE 7

Figs 1–21. *Rhaxeros synaimon* sp. nov.; locality PL1989, Mirrabooka Formation. 1–2, 5, NMV P144863; small cephalon, lateral, anterior and palpebral views; ×4·5. 3, 6, NMV P144888; pygidium, lateral and dorsal views; ×4. 4, 7, 9, NMV P144860; small cranidium with rostral plate, lateral and palpebral views; ×5; rostral plate, ventral view; ×6·25. 8, 11–12, NMV P144847, holotype; cranidium, anterior, palpebral and lateral views; ×2·75. 10, NMV P144890; small cranidium with anteriormost thoracic segment, palpebral view; ×6. 13, NMV P144892; rostral plate, ventral view; ×4·5. 14, NMV P144865; librigenal doublure, ventral oblique view; ×4·5. 15, NMV P144845; incomplete cephalon, oblique view; ×2·75. 16, NMV P144846; incomplete cephalon, palpebral view; ×3·5. 17, NMV P144861; cranidium, palpebral view; ×5·5. 18, 21, NMV P144879; pygidium, posterior and dorsal views; ×3. 19, NMV P144735; first five thoracic segments, dorsal view; ×4·5. 20, NMV P144866; librigena, oblique view; ×5.

PLATE 7



HOLLOWAY and LANE, *Rhaxeros*

Rhaxeros trogodes sp. nov.

Plate 8, figures 1–17, 20

Derivation of name. Greek 'trox' – caterpillar, together with the suffix '-odes' – denoting likeness, referring to the appearance of the exoskeleton.

Holotype. Pygidium NMV P145017, Pl. 8, figs 5, 9, 12; from PL1996.

Paratypes. Incomplete cephala NMV P144981, P144985; cranidia NMV P144975, P144977–P144979, P144983, P144986; incomplete cranidium with partial thorax NMV P144980; librigenae NMV P144987, P144989–P144991, P144993–P144994, P144996, P145002–P145003; rostral plates NMV P145000–P145001, P145004, P145024; hypostomes NMV P144998–P144999, P145006, P145025; incomplete thoraces NMV P144984, P144995, P145007–P145008; pygidia with incomplete thoraces NMV P145010–P145011; pygidia NMV P144974, P144988, P145009, P145014–P145016, P145018, P145023; all from PL1996.

Other material. A large number of disarticulated and mostly disarticulated exoskeletal remains from PL1996; three pygidia from PL3303 and other localities within the Borenore Limestone.

Diagnosis. Cephalon moderately convex; axial furrow dying out anteriorly, preglabellar and lateral border furrows not defined. Librigena with posterior margin very weakly concave forwards and genal angle broadly rounded; eye small, situated almost its own length from posterior cephalic margin. Posterior branch of facial suture barely curved. Connective suture more strongly curved abaxially than adaxially, meeting rostral suture at almost 90°. Pygidium strongly convex, with weak sagittal carina extending for posterior 60 per cent. in plan view; radial ridges and furrows very faint or indistinguishable laterally; holcos absent. Terrace ridges present on anterior 25 per cent. of cranidium, on pygidium restricted to articulating facets.

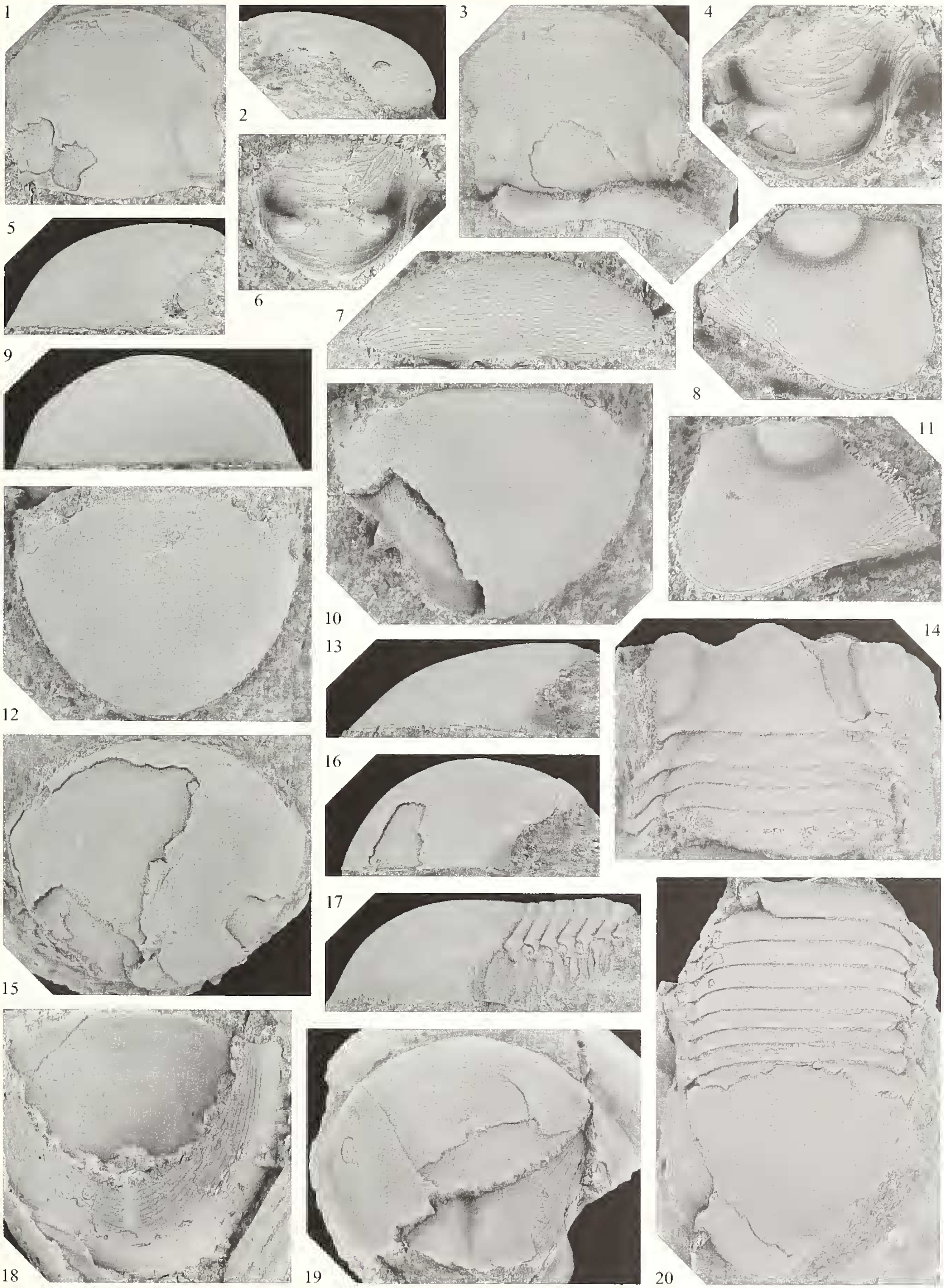
Description. Hypostome with middle body *c.* 150 per cent. as wide anteriorly as long (sag.); anterior lobe comprising 65 per cent. sagittal length of middle body, strongly convex transversely and gently convex sagittally; posterior lobe crescentic, much less convex transversely than anterior lobe, flattened and sloping backwards sagittally, dominated anterolaterally by large, inflated macula; middle furrow dying out abruptly at adaxial extremity of macula. Lateral border furrow deepest at outer end of middle furrow; posterior border furrow very shallow. Lateral border decreasing in convexity (tr.) between anterior wing and shoulder; posterior border very weakly convex, barely increasing in length medially.

Thorax strongly arched transversely; very narrow (tr.), subhorizontal proximal portion of pleurae only slightly interrupting curve of axis and steeply downturned portion of pleurae abaxial to fulcrum; anteriormost

EXPLANATION OF PLATE 8

Figs 1–17, 20. *Rhaxeros trogodes* sp. nov.; locality PL1996, Mirrabooka Formation, unless otherwise indicated. 1–2, NMV P144979; cranidium, palpebral and lateral views; ×4. 3, NMV P144983; cranidium, palpebral view; and NMV P144984; thoracic segment, oblique view; ×4. 4, NMV P145025; hypostome, ventral view; ×8. 5, 9, 12, NMV P145017, holotype; pygidium, lateral, posterior and dorsal views; ×4·75. 6, NMV P144998; hypostome, ventral view; ×8. 7, NMV P145001; rostral plate, ventral view; ×5. 8, NMV P144993; librigena, oblique view; ×5·5. 10, 13, NMV P145018; pygidium, dorsal and lateral views; ×4·75. 11, NMV P144994; librigena, oblique view; ×5·5. 14, NMV P144980; incomplete cranidium with first four thoracic segments, dorsal view; ×4. 15–16, NMV P145050; locality PL3303, Borenore Limestone; largest pygidium, dorsal and lateral views; ×2·25. 17, NMV P145011; incomplete thorax and pygidium, lateral view; ×3. 20, NMV P145010; incomplete thorax and pygidium, dorsal view; ×3.

Figs 18–19. *Rhaxeros synaimon* sp. nov.; locality PL1989, Mirrabooka Formation. 18, NMV P144881; pygidium, latex cast in ventral view showing doublure; ×3. 19, NMV P144887; pygidium, plan view; ×3.



HOLLOWAY and LANE, *Rhaxeros*

segment longer (sag., exsag.) than remainder (Pl. 8, fig. 14). Axis comprising *c.* 70 per cent. of segmental width (tr.); axial furrow firmly impressed, diverging strongly backwards on anterior segments, less strongly on subsequent segments, converging backwards on posterior segment (Pl. 8, fig. 20). Articulating half ring on first segment longer sagittally than ring, from which it is separated by weak, convex-backwards articulating furrow; articulating half rings not differentiated on subsequent segments. Pleurae with articulating flange on anterior margin at fulcrum; this flange most strongly developed on first segment, bounded posteriorly by oblique furrow (Pl. 8, fig. 14). Pleurae beyond fulcrum with broad articulating facet and rounded tip (Pl. 8, fig. 3).

Muscle scars. G0 not clearly seen, but apparently similar in shape and position to that in *R. synaimon.* G1 large, kidney- or bean-shaped, posterior edge opposite middle (exsag.) of lunette, anterior edge level with cephalic midlength (sag.) and extending close to axial furrow. G2 and G3 similar to those of *R. synaimon.* Internal surface of pygidium with traces of axial segmentation anteriorly, defined by three pairs of weak, transverse scars that are comma-shaped abaxially and straight medially. More posteriorly, between about 30 per cent. and 50 per cent. pygidial length in plan view, are two pairs of small, elongated, elliptical or lachrymate scars, with rippled surface in some specimens; adaxial pair of scars slightly larger than abaxial pair and extending farther back.

Remarks. A full description of *R. trogodes* is not warranted as in overall morphology this species is similar to *R. synaimon*; the hypostome and thorax are described as the former is unknown and the latter less completely known in *R. synaimon.* The most obvious differences between *R. trogodes* and *R. synaimon* are the greater convexity of the former, especially in the pygidium, the much smaller and more anteriorly placed eye, and the broadly rounded genal angle. *R. trogodes* also differs from *R. synaimon* in that the cephalic axial furrow is slightly deeper, the posterior section of the facial suture is almost straight, the posterior margin of the librigena is not as concave in outline, the lateral and posterior border furrows are not weakly developed on the librigena, the posterior edge of the rostral plate is not as evenly curved but is transverse medially, radial ribs and furrows are very weak or indistinguishable on the pygidium, there is no holcos, and the sagittal ridge on the pygidial doublure is weaker. In *R. trogodes* the terrace ridges on the front of the cranidium are more closely spaced and extend farther back than in *R. synaimon*, and terrace ridges on the pygidium are restricted to the articulating facets, being absent around the lateral and posterior margins. Most of the differences between *R. trogodes* and *R. synaimon* also serve to distinguish the former from the type species.

Kobayashi and Hamada (1974, p. 50) stated that the two cranidia on which they based their species '*Bumastus*' *subquadratus* were found together with the incomplete thorax and pygidium they described as '*Bumastus* aff. *barriensis*'. We assign all of these specimens to *Rhaxeros* and consider them to be probably conspecific; the short axial furrow shown by Kobayashi and Hamada (1974, text-fig. 2C) in their reconstruction of the pygidium is not evident in the specimen. Also possibly belonging to *Rhaxeros subquadratus* is one of the pygidia assigned by Kobayashi and Hamada (1974, pl. 1, fig. 7) to '*Bumastus*' *glomerosus* (= *Bumastella spiculus*); this pygidium differs from that of *Bumastella* in its greater convexity, the absence of the holcos, and the wider doublure that is convex over much of its width. *Rhaxeros subquadratus* shows similarities to *R. trogodes* in the convexity of the cranidium and pygidium, and possibly in the distribution of terrace ridges on the pygidium, but the specimens are too poorly preserved to judge whether they are conspecific with the material from New South Wales.

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D. J. HOLLOWAY

Invertebrate Palaeontology
Museum of Victoria
PO Box 666E
Melbourne
Victoria 3001, Australia
e-mail dhollow@mov.vic.gov.au

P. D. LANE

Department of Earth Sciences
University of Keele
Staffordshire ST5 5BG, UK
e-mail gga15@esci.keele.ac.uk

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